

Records of the Western Australian Museum



Volume 17 Part 1 1995

Records of the Western Australian Museum

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The *Records of the Western Australian Museum* is published twice a year. A series of *Supplements* are also produced. The *Records* are available for sale and exchange, the current price being \$10 plus postage per part. Each volume comprises four parts. Subscriptions can be taken out for whole volumes at a rate of \$30 plus postage. Supplements can be purchased from the W.A. Museum Bookshop. Prices on request.

Printed and published by the Western Australian Museum
© Western Australian Museum, May 1995
ISSN 0312 3162

Cover: The Narrow-banded Snake, *Simoselaps fasciatus* (Günther, 1872).
Illustration by Jillian Ruse.

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Taxonomy of *Rhinolophus simplex* Andersen, 1905 (Chiroptera : Rhinolophidae) in Nusa Tenggara and Maluku, Indonesia

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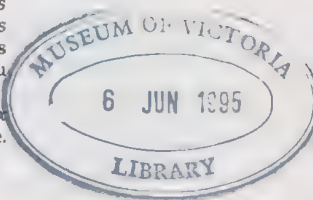
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Abstract – *Rhinolophus simplex simplex* Andersen, 1905 was collected for the first time from Bali, Nusa Penida, Moyo, Sangeang, Rinca, Flores, Lembata, Alor and Sumba islands. Additionally, specimens were collected from Lombok, Sumbawa. Other forms of *R. simplex* were collected from Timor, Savu, Roti, Semau and Kai Kecil islands. *Rhinolophus simplex parvus* Goodwin, 1979 is restricted to Timor Island; *Rhinolophus simplex keyensis* Peters, 1871 occurs on Kai Kecil Island. *Rhinolophus simplex* subsp. nov. is described on the basis of its morphology. It occurs on Savu, Roti and Semau islands.

Protein electrophoresis reveals that populations of *Rhinolophus simplex* show levels of genetic variation that are near the mammalian average. Genetic differentiation of populations is low.



INTRODUCTION

Rhinolophus simplex was described by Andersen (1905) from Lombok I., Nusa Tenggara. Since then it has been considered a species by Corbet and Hill (1980, 1986, 1991); Honacki *et al.* (1982); van Strien (1986) and Tate and Archbold (1939). Koopman (1982), however, considered that *R. simplex* and the closely allied Maluku species: *R. keyensis keyensis* Peters, 1871; *R. k. annectens* Sanborn, 1939; *R. truncatus* Peters, 1871 and *R. nanus* Andersen, 1905 might well be subspecies of *R. megaphyllus* Gray, 1834. Hill (1992) supported this latter view and considered the above forms, along with *R. robinsoni* Andersen, 1918 and *R. megaphyllus thaianus* Hill, 1992 (Thailand) and *R. klossi* Andersen, 1918 (Malaya), as subspecies of *R. megaphyllus*.

Hill (1992) concluded that the major difference between the above forms was in the width of the sella, especially the base, and in the degree of inflation of the median anterior rostral swellings. He considered the forms from New Guinea and Australia and the forms *thaianus*, *robinsoni* and *klossi* from Thailand, have a wide sella and prominent, almost hemispherical narial swellings; in the Maluku forms the sella is a little narrower, but the narial swellings remain well developed; and in the Lesser Sunda island forms both sella and narial swellings are least developed.

Vertebrate surveys by the Western Australian Museum, in collaboration with the Museum Zoologicum Bogoriense, throughout Java, Lesser

Sunda islands and Maluku Tenggara, between 1987 and 1992, resulted in the collection of extensive series of specimens, closely related to *R. simplex*. Additionally a series of *R. borneensis parvus* Goodwin, 1979 (placed as a subspecies of *R. celebensis* by Hill 1992) was collected from Timor.

This paper reports on an examination of morphological and genetic variation among these specimens and on a comparison of this variation with a series of *R. megaphyllus* from Queensland, Australia. A small collection of *R. borneensis importunus* from Java are included for reference.

MATERIALS AND METHODS

A total of 117 adult specimens was examined from a number of islands in Indonesia and Queensland, Australia (see Figure 1 for locality of specimens). They are listed in the "Specimens Examined" section. All these specimens are currently lodged in the Western Australian Museum (WAM). At the completion of this series of surveys half of all the WAM specimens, including the holotype, will be lodged in the Museum Zoologicum Bogoriense, Bogor.

Thirty two measurements of skull, dentary and dental characters and 18 of external characters (all in mm) were recorded from adult specimens (see Figure 2, caption). The skull, dentary and dental characters were measured to an accuracy of 0.01mm, while the external characters were measured to an accuracy of 0.1mm.



Figure 1 Locality of *Rhinolophus simplex* and *R. borneensis* specimens used in this study. ●, *Rhinolophus simplex simplex*; ■, *R. s. parvus*; ★, *R. simplex keyensis*; ▲, *R. simplex subsp. nov.*; and △, *Rhinolophus borneensis importunus*.

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill and Smith (1984). Pelage descriptions follow the colour terminology of Smith (1975).

Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. Additionally two adult age classes were established based on extent of wear on M² hypocone as follows: young adult, no wear or little wear such that the worn area is still elevated above the unworn hypocone basin; for adults, worn surface area of hypocone below level of unworn hypocone basin.

The effect of sex, adult age classes and taxon on skull, dental and external characters was investigated by stepwise multiple regressions on taxon, sex and age for five taxa. These were *Rhinolophus megaphyllus* (Queensland); *R. borneensis importunus* (Java); *R. simplex simplex* (Bali, Nusa Penida, Lombok, Sumbawa, Moyo, Sangeang, Rinca, Flores, Lembata, Alor and Sumba); *R. simplex parvus* (Timor) and *R. simplex subsp. nov.* (Savu, Roti and Semau). *R. simplex keyensis* was not included because the sample size was so small. Further, for the three *R. simplex* subspecies considered, the effect of sex, age and island on skull dental and external measurements was examined using multiple regressions. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Canonical variate (discriminant) analysis (DFA) was computed on skull and external characters separately, with males and females combined, using the SPSS PC⁺ program.

Cellogel electrophoresis of homogenised liver was used to investigate genetically determined protein variation using the techniques described in Richardson *et al.* (1986). This permitted the investigation of variation at 30 presumptive loci.

Genetic variation was assessed on 101 specimens, including some that were juvenile and not included in the morphometric analyses. The proteins scored, with Enzyme Commission Numbers and Locus Symbols in parenthesis, were: aconitate hydratase (E.C.4.2.1.3; *Acon-1* & *Acon-2*), adenosine deaminase (E.C.3.5.4.4; *Ada*), carbonate dehydratase (E.C.4.2.1.1; *Ca*), diaphorase (E.C.1.8.1.4; *Dia*), enolase (E.C.4.2.1.11; *Enol*), fructose-1, 6-diphosphatase (E.C.3.1.3.11; *Fdp*), fumarate hydratase (E.C.4.2.1.2; *Fum*), glucose-6-phosphate dehydrogenase (E.C.1.1.1.49; *G6pd*), glyceraldehyde-3-phosphate dehydrogenase (E.C.1.2.1.12; *Gapd*), guanine deaminase (E.C.3.5.4.3; *Gda*), aspartate aminotransferase (E.C.2.6.1.1; *Got-1* and *Got-2*), α glycerophosphate dehydrogenase (E.C.1.1.1.8; α *Gpd*), glucose-phosphate isomerase (E.C.5.3.1.9; *Gp-1*), isocitrate dehydrogenase (E.C.1.1.1.42; *Idh-1* and *Idh-2*), lactate dehydrogenase (E.C.1.1.1.27; *Ldh-1* and *Ldh-2*), malate dehydrogenase (E.C.1.1.1.37; *Mdh-1* and *Mdh-2*), mannose-phosphate isomerase (E.C.5.3.1.8; *Mpi*), purine nucleoside phosphorylase (E.C.2.4.2.1; *Np*), peptidase (E.C.3.4.13.11; *Pep-A*; E.C.3.4.11.4; *Pep-B*; E.C.3.4.13.11; *Pep-C1* and E.C.3.4.13.9 *Pep-D*), 6-phosphogluconate dehydrogenase (E.C.1.1.44; *6Pgad*), phosphoglucomutase (E.C.5.4.2.2; *Pgm*), superoxide dismutase (E.C.1.15.1.1; *Sod*).

Chi-square was used to test for significance of contingency tables. Tables were reduced when more than a quarter of the cells had expected values less than 2. When expected numbers were small after the tables were reduced to 2 x 2, exact probabilities were computed using twice the probability of the observed tail. Methods used to estimate heterozygosity within populations and genetic distances between populations were those of Nei (1978). These produce "unbiased" estimates. *F*-statistics were computed by the method of Weir and Cockerham (1984), which take into account

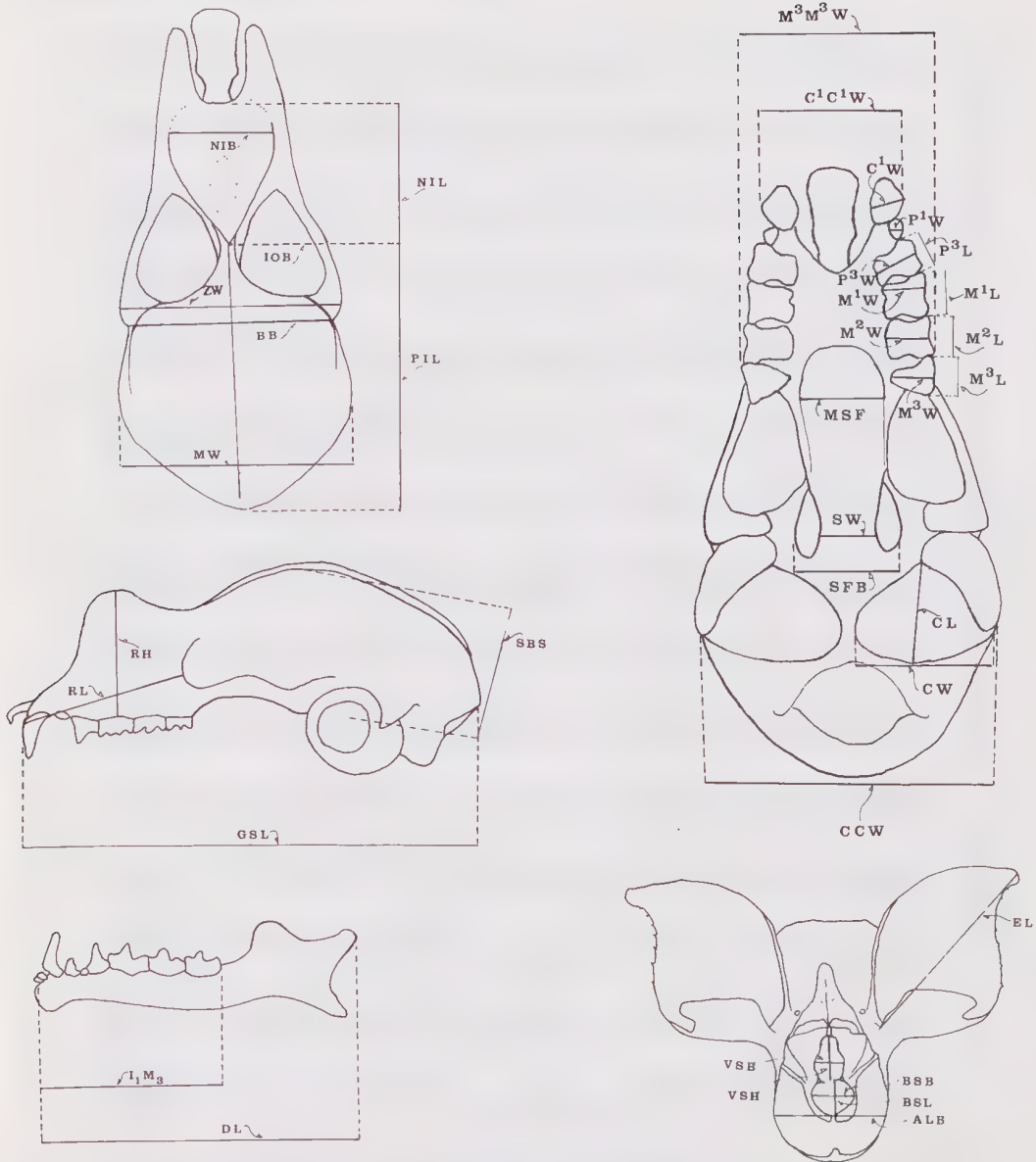


Figure 2 Skull and external measurements referred to in text and their recording points. GSL, greatest skull length; BB, braincase breadth; ZW, zygomatic width; MW, mastoid width; SBS, cranial height – excluding lambdoidal crest; RH, rostrum height – M¹ alveoli to narial crest; RL, rostrum length – orbit anterior edge to maxillary anterior edge; IOB, minimum interorbital breadth; PIL, cranial length – junction of supraorbital and lambdoidal ridges to posteromost point of cranium; NIL, nasal inflation length – from above junction to nares; NIB, lateral narial inflation breadth; MSF, mesopterygoid fossa breadth; SW, sphenoid/pterygoid bridge basal breadth; SFB, sphenorbital fissure maximum breadth; CW, maximum cochlea breadth; CL, cochlea length; CCW, outside cochleae width; M³M³W, outside M³M³ width (cusp); C¹C¹W, outside C¹C¹ basal width (cusp); C¹W, C¹ width (cusp); P¹W, first upper premolar width; P³L, last upper premolar length; P³W, last upper premolar width; M¹L, M¹W, M²L, M²W, M³L and M³W; first, second and third upper molar length and width, respectively; C¹M³L, upper canine to M³ length (cusp); I₁M₃, lower tooth row length (cusp); DL, dentary length – condyle to premaxilla anterior edge; SV, snout to vent length; TV, tail to vent length; EL, ear length; TIB, tibia length; PES, pes length; FA, forearm length; D2M, digit 2 metacarpal length; D3M, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4M, digit 4 metacarpal length; D4P1, digit 4 phalanx 1 length; D4P2, digit 4 phalanx 2 length; ALB, maximum anterior noseleaf breadth; BSL, basal sella length; BSB, maximum basal sella breadth; VSH, vertical sella height; and VSB, maximum vertical sella breadth.

Table 1 Measurements, in mm, (see Figure 2 caption for code to characters) for adult *Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s. parvus*, *R. simplex* subsp. nov. and *R. borneensis importunus*. N, sample size; \bar{X} , mean; SD, standard deviation; min, minimum; max, maximum. (a) skull, dentary and dental characters and (b) external characters; males and females combined.

	GSL	BB	ZW	MW	SBS	RH	RL	IOB	PIL	NIL	NIB	MSF	SW	SFB	CW	CL
<i>R. megaphyllus</i>	N	14	15	15	13	15	15	15	14	15	15	14	15	15	15	15
	\bar{X}	19.53	8.88	9.60	9.32	6.84	6.33	2.63	11.35	5.80	5.55	2.86	1.65	3.24	3.58	3.19
	SD	0.43	0.18	0.24	0.19	0.25	0.27	0.10	0.30	0.31	0.19	0.16	0.12	0.16	0.10	0.10
	Min	18.60	8.55	9.05	9.00	6.40	5.85	2.50	10.65	5.25	5.20	2.55	1.40	2.80	3.40	2.90
	Max	20.00	9.15	10.00	9.55	7.25	6.70	2.85	11.75	6.25	5.80	3.10	1.85	3.50	3.75	3.35
<i>R. simplex simplex</i>	N	47	49	49	47	48	48	49	48	49	49	43	47	46	49	49
	\bar{X}	17.66	7.96	8.73	8.48	5.97	5.60	2.35	10.41	5.23	4.93	2.39	1.37	2.79	3.45	3.03
	SD	0.42	0.20	0.25	0.17	0.32	0.18	0.12	0.32	0.21	0.17	0.12	0.10	0.15	0.13	0.08
	Min	16.75	7.40	8.05	8.05	5.40	5.25	2.10	9.60	4.65	4.60	2.06	1.10	2.50	3.20	2.90
	Max	18.45	8.45	9.15	8.80	6.80	6.10	2.60	11.00	5.65	5.50	2.60	1.60	3.10	3.75	3.20
<i>R. simplex keyensis</i>	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	\bar{X}	17.63	8.05	8.78	8.40	5.93	5.73	2.30	10.40	5.35	4.85	2.58	1.42	2.90	3.55	3.05
	SD	0.18	0.21	0.18	0.07	0.32	0.25	0.14	0.07	0.57	0.64	0.28	0.04	0.07	0.0	0.07
	Min	17.50	7.90	8.65	8.35	5.70	5.55	2.25	10.00	4.90	4.65	2.40	1.40	2.85	3.55	3.00
	Max	17.75	8.20	8.90	8.45	6.15	5.90	2.35	10.80	5.80	5.05	2.75	1.45	2.95	3.55	3.10
<i>R. simplex parvus</i>	N	13	13	13	13	13	13	13	13	13	13	10	13	13	12	12
	\bar{X}	16.87	7.53	8.34	8.14	5.62	5.23	2.20	10.17	4.57	4.55	2.34	1.40	2.75	3.28	2.97
	SD	0.29	0.15	0.13	0.18	0.35	0.18	0.13	0.24	0.28	0.11	0.07	0.12	0.08	0.11	0.09
	Min	16.50	7.20	8.08	7.79	5.10	5.00	2.04	9.75	4.20	4.35	2.20	1.16	2.60	3.10	2.85
	Max	17.30	7.75	8.57	8.49	6.20	5.65	2.38	10.50	5.00	4.75	2.45	1.60	2.90	3.40	3.10
<i>R. simplex</i> subsp. nov.	N	26	27	26	26	27	28	28	27	28	28	23	27	27	27	27
	\bar{X}	15.95	7.11	7.71	7.67	5.57	5.06	2.07	9.52	4.57	4.41	2.27	1.28	2.58	3.17	2.86
	SD	0.50	0.29	0.34	0.26	0.35	0.23	0.11	0.33	0.20	0.17	0.14	0.07	0.11	0.09	0.11
	Min	15.30	6.60	7.25	7.25	4.75	4.65	1.90	9.00	4.20	4.10	2.05	1.15	2.35	3.00	2.70
	Max	17.10	7.65	8.40	8.20	6.40	5.55	2.30	10.25	4.95	4.80	2.50	1.40	2.80	3.40	3.15
<i>R. borneensis importunus</i>	N	9	10	9	10	9	10	10	9	10	9	10	9	8	9	10
	\bar{X}	19.2	8.67	9.72	9.08	6.43	6.10	2.34	11.55	5.07	5.26	2.74	1.59	2.89	3.54	3.06
	SD	0.50	0.25	0.19	0.19	0.25	0.18	0.31	0.14	0.44	0.19	0.08	0.09	0.16	0.09	0.08
	Min	18.50	8.20	9.45	8.85	5.90	5.75	2.10	10.50	4.75	5.05	2.60	1.40	2.70	3.45	2.90
	Max	19.80	8.95	10.00	9.40	6.70	6.40	2.60	11.95	5.26	5.40	2.80	1.70	3.20	3.70	3.20

Table 1 (continued)

[illegible]

Table 1 (continued)

	SV	TV	EL	TIB	PES	FA	D2M	D3M	D3P1	D3P2	D4M	D4P1	D4P2	ALB	BSL	BSB	VSH	VSB
<i>R. megaphyllus</i>																		
N	15	15	15	15	15	14	15	15	15	15	15	15	15	15	12	11	13	15
\bar{X}	47.2	24.1	19.4	19.1	8.3	46.9	35.1	32.9	13.5	19.9	34.5	10.2	12.1	9.0	2.5	3.1	4.4	2.2
SD	2.5	2.1	0.8	0.6	0.3	0.7	0.7	0.6	0.4	0.8	0.6	0.4	0.5	0.6	0.3	0.4	0.3	0.2
Min	42.6	20.9	17.6	17.5	7.4	45.8	33.3	31.9	12.7	18.1	33.5	9.8	11.3	7.7	2.0	2.7	3.7	1.8
Max	51.1	28.0	20.6	20.1	8.6	48.1	36.0	34.1	14.0	21.2	35.6	10.7	12.8	9.6	2.9	4.0	5.1	2.7
<i>R. simplex simplex</i>																		
N	49	49	49	48	49	48	48	49	49	49	49	49	49	49	39	38	40	47
\bar{X}	43.2	21.1	17.7	18.2	7.6	41.9	31.4	29.5	12.3	19.1	30.3	8.8	11.8	8.1	2.3	2.5	3.9	2.0
SD	1.5	2.0	1.0	0.7	0.4	1.3	1.4	1.0	0.6	0.9	1.1	0.4	0.6	0.5	0.2	0.2	0.2	0.2
Min	39.9	18.1	14.4	16.0	6.1	39.0	28.7	27.1	11.0	17.1	27.5	7.5	10.5	7.2	1.8	2.1	3.2	1.7
Max	46.6	26.2	19.6	19.7	8.4	44.9	35.6	31.8	13.7	21.0	32.8	9.9	13.1	9.3	2.7	3.1	4.3	2.4
<i>R. simplex keyensis</i>																		
N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
\bar{X}	42.7	18.7	18.9	16.8	7.3	41.4	31.1	28.5	11.7	19.0	30.0	8.9	11.0	9.2	2.7	2.8	4.5	2.4
SD	1.2	2.2	1.7	0.1	0.0	0.1	0.2	0.5	0.4	0.1	0.9	0.1	0.2	0.5	0.4	0.4	0.0	0.4
Min	41.8	17.2	17.7	16.7	7.3	41.4	31.0	28.2	11.4	19.0	29.4	8.8	10.9	8.8	2.4	2.6	4.5	2.1
Max	43.5	20.3	20.0	16.9	7.3	41.5	31.3	28.9	11.9	19.1	30.7	9.0	11.1	9.5	2.9	3.1	4.5	2.7
<i>R. simplex parous</i>																		
N	13	12	13	13	13	13	12	12	13	12	12	13	13	13	13	13	13	13
\bar{X}	37.7	20.1	16.1	17.3	7.7	40.1	29.9	27.9	11.6	17.2	28.7	8.3	10.9	7.4	1.9	2.5	3.4	1.9
SD	1.2	2.2	0.4	0.6	0.5	0.8	0.7	1.0	0.4	0.5	0.9	0.3	0.4	0.3	0.2	0.1	0.3	0.1
Min	35.4	17.0	15.4	16.5	6.8	38.2	28.6	26.8	10.9	16.2	27.7	7.8	10.3	7.0	1.6	2.3	3.1	1.6
Max	39.7	23.8	16.6	18.5	8.3	41.3	31.1	30.2	12.3	18.0	30.5	8.5	11.8	7.8	2.2	2.7	4.0	2.0
<i>R. simplex subsp. nov.</i>																		
N	28	28	28	28	28	27	28	28	28	28	28	28	28	21	16	15	16	24
\bar{X}	38.2	20.3	16.7	15.2	6.4	37.4	27.6	26.3	10.3	16.2	26.7	7.9	9.8	7.6	2.3	2.4	3.6	1.9
SD	1.7	1.8	0.8	0.8	0.3	0.9	1.0	0.8	0.5	0.8	0.9	0.3	0.8	0.4	0.2	0.2	0.3	0.2
Min	35.6	18.0	15.0	14.0	5.9	35.8	26.1	24.8	9.5	14.7	24.6	7.5	8.4	6.8	2.0	2.2	3.3	1.6
Max	42.8	24.3	18.3	16.6	7.1	39.1	29.5	27.6	11.4	18.4	28.5	8.5	11.4	8.8	2.6	2.7	4.2	2.1
<i>R. borneensis importunus</i>																		
N	10	10	10	10	10	9	10	10	10	10	10	10	10	10	9	9	10	10
\bar{X}	45.7	23.8	19.4	19.9	9.3	44.4	32.3	30.3	13.0	20.7	31.7	9.3	12.7	9.0	2.5	2.6	4.5	2.1
SD	2.4	2.3	0.54	0.9	0.4	1.0	1.1	0.9	0.5	1.0	1.2	0.4	0.6	0.3	0.2	0.2	0.3	0.1
Min	40.8	19.0	18.7	18.3	8.4	42.4	29.9	28.4	12.1	18.7	29.1	8.5	11.6	8.6	2.2	2.2	4.1	1.9
Max	48.1	26.9	20.4	21.1	9.7	45.5	33.6	31.3	13.6	22.1	33.3	10.0	13.6	9.4	3.0	2.8	5.0	2.2

sample size variation. Cluster analysis used the UPGMA method of Sneath and Sokal (1973). All statistical analyses were undertaken with Genstat 5 (Genstat 5 Committee 1987) and Biosys-1 (Swofford and Selander 1989).

MORPHOLOGY: STATISTICS

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size of each taxon are presented in Table 1 for (a) skull, dentary and dental characters and (b) external characters

Multiple regressions

Multiple regressions were run for skull, dentary and dental characters and external characters on sex and adult age for five taxa (*R. borneensis*, *R. megaphyllus*, *R. simplex simplex*, *R. s. parvus* and *R. s. subsp. nov.*). Additionally, multiple regression was run for the *R. simplex* group alone for skull and external characters on sex, adult age and island. In these analyses, islands with small sample size were omitted because either a sex or adult age category was absent. The results of these analyses are presented in Tables 2 and 3.

In the following discussions, because of the large number of interactions being tested, the level of significance was set at $P < 0.01$.

All 5 taxa – skulls

Sex. From Table 2a, eight characters (greatest skull length, GSL; braincase breadth, BB; rostrum height, RH; rostrum length, RL; outer cochlear width, CCW; upper maxillary tooth row length, C¹M³L; lower tooth row length, I¹M³L and dentary length, DL) showed a significant relationship with sex alone ($P < 0.000$ – $P = 0.002$). Also there was a significant interaction for outer M³M³ width for sex, age and taxon ($P = .009$). This interaction resulted from subadult females being smaller than subadult males in *R. megaphyllus* and females being slightly smaller than males in *R. s. parvus* and *R. borneensis*.

Age. Rostrum height, RH; showed a significant ($P = 0.003$) relationship with age alone. Outer M³M³ width also had a significant interaction between age, sex, and taxon ($P = 0.009$), as discussed above.

Taxon. All skull characters, except M³ width, had a significant relationship ($P < 0.001$) with taxon. These relationships were consistent between the sex and age groupings; the only significant interaction was between sex, age and taxon ($P = 0.009$) for outer M³M³ width, as discussed above, clearly there is a considerable extent of morphological distinctness among these taxa.

All 5 taxa – externals

Sex and age. There were significant relationships with snout to vent length, SV, both with sex alone

($P < 0.001$) and age alone ($P < 0.007$) and with interactions between sex and age and sex and taxon (Table 2b).

Taxon. All characters were significantly related to taxon ($P < 0.001$), except basal sella length (BSL).

R. simplex group – skulls

Sex. No character had a significant relationship with sex alone, although there was a significant interaction between age, sex and island ($P = 0.005$ and $P = 0.002$, respectively) for braincase breadth BB and M² width, M²W. For BB, this resulted from young adult females being larger than old adult females on Roti I., and males being larger than females on Moyo and Flores, whereas on other islands they were approximately the same size, For M²W, young adult males were larger than old adult males on Flores and young adult males were larger than young adult females on Savu I., whereas on other islands they were approximately the same size. Also, for P¹ width, P¹W, there was a significant interaction between sex and island ($P = 0.008$) which resulted from females being larger than males on Savu I., whereas on other islands they were approximately the same size.

Age. No character had a significant relationship with age alone. But there were significant interactions for BB and M²W between sex, age and island, as discussed above.

Island. All 30 characters had a significant relationship with island alone, most at $P < 0.001$. These relationships were consistent for sex and age categories except for braincase breadth, M² width, and P¹ width which had interactions between age and or sex and island, as discussed above.

Clearly, there was marked morphological differences among the island populations of *R. simplex*.

R. simplex group – externals

Sex and age. The only significant relationship was the interaction between sex and island for ear length, EL (Table 3b). This resulted from the Rotinese sample where males had greater ear lengths than females, whereas on other islands they were subequal.

Island. All characters except ear length, EL; maximum anterior noseleaf breadth, ALB, and maximum basal sella breadth, BSB, were significant, most at $P < 0.001$. The only significant interaction was again between sex and island for ear length (Table 3b) as discussed above.

Multivariate analyses

5 taxa analysis

Canonical variate (discriminant) analysis (DFA) was carried out on five taxa (*R. megaphyllus*, *R.*

Table 2 Multiple regressions on taxon (*Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s parvus*, *R. simplex* subsp. nov. and *R. borneensis importunus*), sex and age for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. Significance levels are *, 0.05>p>0.01; ** 0.01>p>0.001; and *** p<0.001.

Table 2a

Character	Sex	Main Effects Age	Taxon	Sex. Age	Interactions Sex. Taxon	Age. Taxon	Sex. Age. Taxon
GSL	**		***				
	7.167	3.325	128.719	0.099	0.779	0.753	0.833
BB	***	*	***				
	11.472	4.116	155.075	0.235	0.778	0.416	0.402
ZW			***				
	3.798	1.783	127.417	0.060	0.350	0.162	1.240
MW	*		***				
	6.635	1.952	133.256	0.358	0.259	0.248	2.249
SBS			***				
	1.445	0.487	26.914	0.009	0.785	0.767	0.511
RH	***	**	***				
	11.602	9.752	64.575	0.280	0.843	0.710	1.640
RL	***		***				
	11.100	1.294	80.190	0.355	2.222	0.805	1.848
IOB			***				
	.696	.904	25.446	0.932	0.856	0.982	0.898
PIL			***				
	0.206	0.960	48.550	0.705	0.355	0.538	0.563
NIL			***				
	1.717	0.314	34.673	2.103	0.160	0.165	1.253
NIB	*		***				*
	7.064	0.756	88.723	0.832	0.543	0.332	3.993
SW			***				
	0.536	0.728	23.096	2.803	1.786	1.136	1.340
SFB			***				
	0.908	0.930	29.172	2.802	0.879	0.472	0.560
CW			***				
	0.177	0.106	20.200	0.839	0.308	0.666	0.360
CL			***				
	0.288	0.248	23.949	2.588	0.644	0.443	0.864
CCW	**	*	***				*
	9.626	6.572	63.086	0.125	0.753	0.353	4.005
M ³ M ³ W			***				**
	3.631	0.778	156.608	0.230	1.114	0.745	5.091
C ¹ W			***				
	0.152	0.000	31.014	3.093	1.208	1.130	1.907
P ¹ W			***				*
	0.062	0.599	13.425	1.258	1.741	2.065	3.510
P ³ L			***	*			
	0.444	0.079	59.942	6.123	0.322	1.179	2.854
P ³ W			***				
	0.375	0.003	29.514	2.202	0.365	0.670	0.931
M ¹ L			***				
	0.223	0.785	68.903	0.628	0.240	0.589	1.007
M ¹ W			***				
	0.105	0.619	21.441	0.904	0.610	0.257	0.743
M ² L			***				
	0.244	0.047	63.528	0.104	0.894	1.121	0.626
M ² W			***				
	3.792	1.159	41.020	1.011	1.367	0.459	1.168
M ³ L			***	*			
	0.746	0.038	59.181	4.298	0.802	0.901	1.700
M ³ W			*				
	0.679	2.183	1.720	6.084	1.125	0.706	1.081
C ¹ M ³ L	**		***				*
	8.473	1.459	116.743	0.000	0.305	0.637	3.323
I ₁ M ₃ L	**	*	***				
	9.751	5.077	112.654	3.117	1.500	0.684	3.078
DL	**		***				
	10.616	2.973	144.502	0.015	1.092	1.165	2.409
DEGREES OF FREEDOM	1,71	1,71	4,71	1,71	4,71	4,71	2,71

Table 2b

Character	Sex	Main Effects Age	Taxon	Sex. Age	Interactions Sex. Taxon	Age. Taxon	Sex. Age. Taxon
SV	*** 15.293	** 7.898	*** 40.602	** 7.900	** 5.050	2.188	2.307
TV	0.257	2.221	** 5.135	0.019	0.514	1.982	0.624
EL	0.083	0.003	*** 14.580	0.001	0.309	0.412	0.067
TIB	0.662	0.290	*** 48.605	0.269	1.402	1.398	1.326
PES	0.847	0.440	*** 59.904	0.005	0.505	0.573	1.163
FA	0.206	0.173	*** 77.969	3.968	1.403	0.609	0.960
D2M	0.381	0.137	*** 47.522	0.290	1.241	0.486	1.121
D3M	0.002	0.084	*** 55.055	1.323	1.162	0.927	1.142
D3P1	0.348	3.552	*** 41.778	0.884	1.388	1.112	1.485
D3P2	0.468	0.733	*** 34.810	0.001	1.831	1.926	0.093
D4M	0.751	0.737	*** 78.263	1.460	2.230	1.571	1.380
D4P1	1.229	0.055	*** 52.247	1.843	2.900	0.892	2.660
D4P2	2.259	1.882	*** 27.121	0.711	1.768	1.225	1.513
ALB	2.217	2.987	*** 15.412	0.134	0.346	1.688	0.112
BSL	0.601	0.567	2.120	0.057	0.487	0.562	0.607
BSB	2.481	0.165	*** 11.389	0.142	1.086	1.312	0.834
VSH	1.135	0.002	*** 17.864	2.984	2.412	1.344	1.169
VSb	0.062	0.311	** 5.624	1.748	0.363	0.319	0.282
DEGREES OF FREEDOM	1,59	1,59	4,59	1,59	4,59	4,59	2,59

borneensis importunus, *R. simplex simplex*, *R. s. parvus* and *R. simplex* subsp. nov.). *Rhinolophus s. keyensis* was included in this analyses but unallocated because of its small sample size (N = 2). Both sex and age groups were combined. However, this analysis was carried out only after deleting nine skull characters shown in the multiple regression analysis to be significantly (P<0.01) influenced by sex or age (GSL, BB, RH, RL, CCW, M³M³W, C¹M³L, I¹M³L, DL, see Table 2a). Also MSF, and C¹C¹B were deleted because too many individuals had these values missing. The skull analyses used was with this reduced set of 21 characters.

Similarly, the DFA of external characters was run following deletion of snout to vent length, SVL, because there were significant (P<0.01) interactions between sex and age for this character (Table 3b).

Skulls. The DFA for the five taxa was first run using the reduced set of 21 characters and using islands as the *a priori* grouping. When these islands were grouped to represent the five above taxa the configuration of the taxon clusters in discriminate

function space was very similar. However, because the number of individuals in some taxa was less than the number of characters measured (*R. borneensis*, 8; *R. megaphyllus*, 15) a reduced set of characters was used in the analysis. Of the 21 characters used in the DFA of the five taxa as the *a priori* groups, five were chosen because they provided values that minimise Wilk's Lambda. The plots of the discriminant functions 1 to 3, based on the reduced set of five characters (mastoid width, MW, supraorbital length, NIL; M¹ length, M¹L; zygomatic width, ZW; and sphenorbital fissure width, SFB) produced very similar plots to the above analyses, and so only these are presented and discussed below.

The DFA produced three significant canonical functions. These three functions combined explained 99.9 percent of the variance (Table 4a) with function 1, 86.9 percent; function 2, 10.2 percent and function 3, 2.8 percent. A total of 95.3 percent of individuals were correctly classified to their appropriate taxon. Only five individuals were

Table 3 Multiple regressions for *Rhinolophus simplex* (*R. s. simplex*, *R. s. parvus* and *R. s. subsp. nov.*) on island, sex, and age for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. Significance levels as for Table 2.

Table 3a

Character	Sex	Main Effects		Sex. Age	Interactions		
		Age	Island		Sex. Island	Age. Island	Sex. Age. Island
GSL	0.044	0.458	*** 41.595	* 6.347	2.615	1.226	* 7.697
BB	0.117	3.417	*** 44.800	* 6.416	* 3.439	** 5.126	** 9.171
ZW	0.008	0.434	*** 42.519	3.626	2.658	0.972	* 5.708
MW	0.091	* 6.843	*** 51.452	* 7.087	* 3.796	1.288	* 6.800
SBS	0.000	0.140	*** 3.796	0.316	1.553	0.425	0.558
RH	2.826	0.262	*** 9.135	1.928	0.513	0.514	* 5.024
RL	0.134	0.045	*** 31.389	1.377	* 3.429	1.099	0.138
IOB	0.246	1.130	*** 9.576	1.452	0.591	0.713	0.933
PIL	0.334	0.869	*** 14.320	1.778	0.615	1.082	3.382
NIL	0.003	0.843	*** 18.056	2.770	1.767	0.985	0.159
NIB	0.031	0.275	*** 28.287	1.499	* 3.256	1.126	1.882
SW	1.053	1.376	** 4.973	0.022	1.417	2.335	0.259
SFB	1.533	2.395	*** 2.584	1.533	1.422	0.268	2.228
CW	0.001	1.339	*** 6.148	0.209	0.778	0.549	0.952
CL	0.011	0.864	*** 8.179	2.401	2.036	0.795	0.311
CCW	2.615	0.604	*** 20.927	0.075	0.805	0.160	0.391
M ³ M ³ W	0.482	1.273	*** 46.851	* 5.092	1.704	0.978	* 4.591
C ¹ W	1.008	0.021	** 4.858	0.021	0.142	0.542	0.110
P ¹ W	1.404	* 5.953	*** 14.556	0.005	** 4.348	* 3.014	1.157
P ³ L	0.273	0.673	*** 17.219	0.006	0.334	* 3.251	0.268
P ³ W	0.154	1.042	*** 13.061	1.042	1.109	0.582	0.155
M ¹ L	0.424	0.832	*** 26.398	2.055	2.001	2.654	2.921
M ¹ W	0.872	0.000	*** 5.539	0.000	2.406	1.533	0.058
M ² L	0.709	0.709	*** 10.628	1.971	0.847	0.194	1.784
M ² W	1.919	1.161	*** 8.432	* 6.848	0.926	0.618	** 11.323
M ³ L	0.003	3.193	*** 11.674	0.163	1.317	0.642	0.127
M ³ W	0.129	0.517	*** 11.120	2.068	1.255	1.550	0.389
C ¹ M ³ L	0.353	0.353	*** 51.854	1.411	1.352	0.177	* 4.332
I ₁ M ₁ L	0.315	0.013	*** 73.172	0.617	1.427	0.479	2.521
DL	0.014	0.047	*** 66.467	2.620	2.465	1.218	* 6.367
DEGREES OF FREEDOM	1,26	1,26	5,26	1,26	4,26	4,26	1,26

Table 3b

Character	Sex	Main Effects		Sex. Age	Interactions		
		Age	Island		Sex. Island	Age. Island	Sex. Age. Island
SV	0.176	0.069	*** 28.275	0.150	0.520	0.694	2.084
TV	0.284	2.670	* 3.109	0.413	1.036	1.862	0.420
EL	0.098	0.063	1.798	0.004	** 5.505	2.437	* 4.712
TIB	0.005	0.083	*** 41.150	0.926	0.281	0.365	1.472
PES	0.116	0.040	*** 12.590	0.904	0.917	0.912	0.818
FA	0.543	1.035	*** 24.474	1.183	0.838	0.931	3.275
D2M	0.532	0.000	*** 17.119	1.075	0.543	0.770	1.490
D3M	0.072	1.232	*** 14.872	1.342	0.547	0.679	0.249
D3P1	1.012	0.124	*** 15.439	0.000	1.498	0.608	0.209
D3P2	0.799	1.046	*** 17.561	0.199	0.880	0.426	0.002
D4M	0.402	3.601	*** 33.937	* 4.652	2.621	1.614	1.607
D4P1	* 4.457	0.012	*** 13.284	1.016	2.557	0.866	0.019
D4P2	0.041	0.157	*** 17.845	2.890	0.379	0.922	* 5.557
ALB	0.000	0.583	2.459	0.055	1.251	1.045	0.018
BSL	0.094	0.165	** 4.530	1.108	0.073	1.021	1.099
BSB	0.932	0.007	0.699	1.916	0.533	1.302	* 5.935
VSH	0.115	0.490	*** 8.392	3.426	1.103	0.692	2.510
VSB	0.580	* 5.218	* 2.924	0.205	0.294	1.351	0.381
DEGREES OF FREEDOM	1,23	1,23	5,23	1,23	3,23	4,23	1,23

incorrectly classified: Four *R. simplex* sp. nov. were classified as *R. s. parvus* and one *R. s. simplex* was classified as *R. s. parvus*.

The plot of functions 1 and 2 most clearly separates the taxa (Figure 3a) and plots of other combinations of functions 1–3 do not further clarify graphically this separation. From Figure 3a, the *R. borneensis* and *R. megaphyllus* clusters are clearly separate on function 2 and these two species clearly cluster separately from the *R. simplex* subspecies on function 1. Further, the *R. simplex* subspecies clusters, which partially overlap, separate on function 1. The unallocated *Rhinolophus s. keyensis* grouped closely with *R. s. simplex*.

The character loading most heavily (>0.5) on function 1 and which is presumed an important discriminant between *R. borneensis*, *R. megaphyllus* and *R. simplex*, and among the *R. simplex* subspecies, was M' length (Table 4a). The characters loading heavily (>0.5) on function 2 and

presumed important in discriminating between *R. borneensis* and *R. megaphyllus* were supraorbital length, NIL, and zygomatic width, ZW (Table 4a).

Externals. The DFA for the five taxa was first run using the reduced set of 17 characters and using island as the *a priori* grouping. When these islands were grouped to represent the five above taxa the configuration of the taxon clusters in discriminant function space was very similar to that produced above. However, because the number of individuals in some taxa was less than the number of characters measured (e.g. *R. borneensis*, 9; *R. megaphyllus*, 12) fewer characters were used in the analysis. Five the 17 characters used in the DFA as the *a priori* groups were selected (forearm length, FA; pes length, PES; vertical sella height VSH; digit 4, phalanx 1 length, D4P2) for analysis because they provided values that minimise Wilk's Lambda. These five characters produced similar DFA plots to those from the 17 characters. Only the DFA

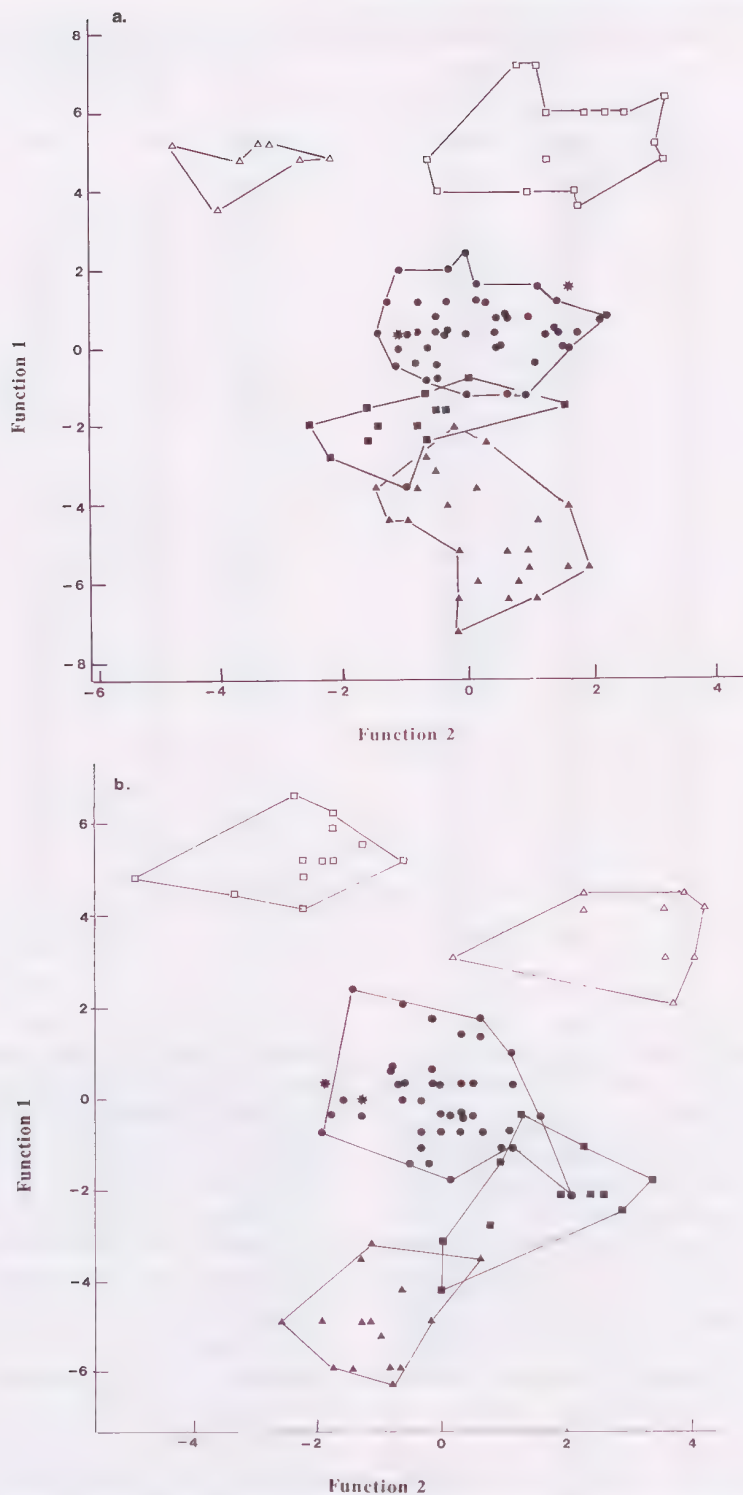


Figure 3 Canonical variate analysis grouped by taxon (*Rhinolophus megaphyllus*, \square ; *R. simplex simplex*; *R. s. parvus*; *R. s. subsp. nov.*; and *R. borneensis importunus*) based on (a) skull, dentary and dental characters and (b) external characters, for functions 1 and 2. Other taxon symbols as for Figure 1 caption.

Table 4 Canonical variate function coefficients for the five taxa: *Rhinolophus megaphyllus*, *R. simplex simplex*, *R. s. parvus*, *R. s. subsp. nov.* and *R. borneensis parvus*. *R. s. keyensis* unallocated. Standardised values, followed by (in brackets) unstandardised values. (a) skull and dental; (b) external characters.

Table 4a

Character	Function 1		Function 2		Function 3	
MW	0.3517	(1.7477)	0.4891	(2.4302)	0.6221	(3.0911)
NIL	0.2224	(0.9304)	0.7231	(3.0253)	-0.7308	(-3.0575)
M'L	0.5114	(8.5400)	-0.4025	(-6.7206)	-0.1993	(-3.3275)
ZW	0.3518	(1.3538)	-0.8787	(-3.3811)	-0.4380	(-1.6854)
SFB	0.1374	(0.9804)	0.4699	(3.3522)	0.7509	(5.3568)
CONSTANT		-45.9212		-6.4634		-6.3208
VARIATION EXPLAINED (%)	86.9		10.2		2.8	

Table 4b

Character	Function 1		Function 2		Function 3	
FA	0.6108	(0.5706)	-0.1597	(-0.1492)	-0.1565	(-0.1462)
PES	0.2590	(0.7415)	1.0000	(2.8640)	-0.4652	(-1.3324)
VSH	0.3455	(1.2204)	-0.2507	(-0.8854)	0.2965	(1.0471)
D4P2	-0.1158	(-0.1892)	0.2766	(0.4519)	1.1051	(1.8054)
D4M	0.3276	(0.3474)	-0.6520	(-0.6915)	-0.1803	(-0.1912)
CONSTANT		-42.6952		3.4166		-2.7095
VARIATION EXPLAINED (%)	77.3		16.6		4.1	

based on this reduced set of five characters are presented and discussed below.

The DFA produced four significant canonical functions. These functions combined explained 100 percent of the variance (Table 4b) with function 1, 77.3 percent; function 2, 16.6 percent; function 3, 4.1 percent and function 4, 2.0 percent. A total of 95.6 percent of individuals was correctly classified to their appropriate taxon. Four specimens were incorrectly classified. One *R.s. subsp. nov.* was classified as *R.s. parvus*, one *R.s. parvus* was classified as *R.s. subsp. nov.* and two *R.s. simplex* were classified as *R.s. parvus*.

The plot of functions 1 and 2 and functions 1 and 3 most clearly separates the taxa (Figure 3b) and plots of other combinations of functions 1–4 does not further clarify graphically this separation. From Figure 3b, *R. borneensis*, *R. megaphyllus*, *R.s. simplex* and *R.s. subsp. nov.* cluster separately on function 1 with *R.s. parvus* also clustering separately from *R. megaphyllus* and *R. borneensis* on this function.

Additionally *R. megaphyllus* clusters separately from both *R.s. parvus* and *R. borneensis* on function 2. The unallocated *R. simplex keyensis* specimens cluster close to *R. s. simplex*.

The character loading most heavily (>0.6) on function 1, which is presumed to be a most important discriminant between most of these taxon, was forearm length (Table 4b). the characters loading heavily (>0.6) on function 2, and presumed important discriminants between *R. megaphyllus* and both *R.s. parvus* and *R. borneensis*

were pes length, PES, and digit 4 metacarpal length, D4M (Table 4b).

R. simplex analysis

A DFA was carried out on the three subspecies of *R. simplex* (*R.s. simplex*, *R.s. parvus*, and *R. s. subsp. nov.*) after combining both sex and age groups. This analysis was carried out for skulls, dentary and dental characters only after deleting three skull characters shown by the multiple regression analysis to be significantly ($P<0.01$) influenced by sex or age (BB, P'W, and M'W, see Table 3a). Also, MSF and C'C'W were deleted because too many individuals had these values missing. The skull analyses was then run with the reduced set of 25 characters.

Similarly the DFA of external characters was run after deletion of ear length from the analysis because there was a significant ($P<0.01$) interaction between sex and island for this character (Table 3b).

Skulls. The DFA for the *R. simplex* subspecies was first run using the reduced set of 25 characters and using islands as the *a priori* groupings. When these islands were then grouped to represent the three taxa *R. s. simplex*, *R. s. parvus* and *R. s. subsp. nov.* (*R. s. keyensis* unallocated), the configuration of the taxon clusters in discriminant function space was similar to that produced above. However, as the number of characters was considerably larger than the number of individuals in one taxon group (*R. simplex parvus*, 12) a reduced set of five characters

Table 5 Canonical variate functions coefficients for the three subspecies of *Rhinolophus simplex* (*R. s. simplex*, *R. s. parvus*, *R. s. subsp. nov.*). *Rhinolophus s. keyensis* unallocated. Standardised values, followed by (in brackets) unstandardised values (a) skull and dental; (b) external characters.

Table 5a

Character	Function 1		Function 2	
I ₁ M ₃ L	1.2760	(5.8790)	-0.9938	(-4.5787)
C ¹ M ³ L	-0.8948	(-4.4169)	1.0576	(5.2205)
M ³ M ³ W	0.1955	(1.1858)	0.8975	(5.4438)
CB	0.4427	(3.8282)	0.2631	(2.2755)
NIB	0.2770	(1.6894)	-0.4586	(-2.7968)
CONSTANT		-42.6169		-27.1418
VARIATION EXPLAINED (%)	75.4		24.6	

Table 5b

Character	Function 1		Function 2	
TIB	0.4414	(0.6271)	-0.4069	(-0.5781)
SV	0.9602	(0.6010)	0.6795	(0.4506)
PES	0.3907	(1.1571)	-0.8443	(-2.5005)
D4P1	0.4708	(1.3476)	0.4592	(1.3145)
VSH	0.6294	(3.3753)	0.0508	(0.2722)
TV	-0.5209	(-0.2470)	0.1439	(0.0682)
BSB	-0.5409	(-2.5337)	0.3179	(1.4891)
CONSTANT		-50.4099		-6.9463
VARIATION EXPLAINED (%)	85.4		14.6	

was selected on the basis that they provided values that minimise Wilk’s lambda. The plots of the discriminant function 1 and 2 based on this reduced set of five characters (lower, tooth row length, I₁M₃L; upper maxillary tooth row length, C¹M³L; outer M³M³ width, M³M³W; cranium breadth, CB; and nasal inflation breadth, NIB) produced very similar plots to the above analyses, and so only these are presented and discussed below.

The DFA produced two significant canonical functions. Function 1 explained 75.4 percent of the variance and function 2, 24.6 percent (Table 5a). A total of 100 percent of individuals were correctly classified to their appropriate subspecies. The plot of function 1 and 2 (Figure 4a) clearly separates the subspecies: *simplex*, *parvus* and *subsp. nov.* with the unallocated *keyensis* grouping with *simplex*. Function 1 separates all three allocated subspecies clusters and function 2 partially separates *R. s. simplex* from both *R. s. parvus* and *R. s. subsp. nov.* and completely separates the *R. s. parvus* and *R.s. subsp. nov.* clusters.

The characters loading most heavily (>0.8) on function 1 and presumed important discriminants between the three allocated subspecies, were lower tooth row length, I₁M₃L, and upper maxillary tooth row length, C¹M³L (Table 5a). Characters loading most heavily on function 2 (>0.8) and presumed particularly important in discriminating between *R. s. parvus* and *R. s. subsp. nov.* included, in

addition to the above two characters, outer M³M³ width, M³M³W (Table 5a).

Externals. The DFA for the *R. simplex* subspecies was first run using the reduced set of 17 characters and using islands as the *a priori* groupings. When these islands were then grouped to represent the three allocated *R. simplex* subspecies (see above), the configuration of the taxon clusters in discriminant function space was similar to that produced above. However, because the number of characters was larger than the number of individuals in one taxon group (*R. simplex parvus*, 12) a reduced set of seven characters was selected (tibia length, TIB; snout to vent length, SV; pes length, PES; digit 4, phalanx 1 length, D4P1; vertical sella breadth, VSB; tail to vent length, TV; basal sella breadth, BSB) using the method for skulls above; this produced similar DFA plots to those produced using the 17 characters. Only the DFA based on this set of seven characters are presented and discussed below.

The DFA produced two significant canonical functions. Function 1 explained 85.4 percent of the variance and function 2, 14.6 percent (Table 5b). A total of 100 percent of individuals were correctly classified to their appropriate subspecies. The plot of functions 1 and 2 (Figure 4b) clearly separates the subspecies, with the unallocated *keyensis* again grouping with *R. s. simplex*. Function 1 separates all three subspecies clusters and function 2 separates *R.s. parvus* and *R.s. subsp. nov.*

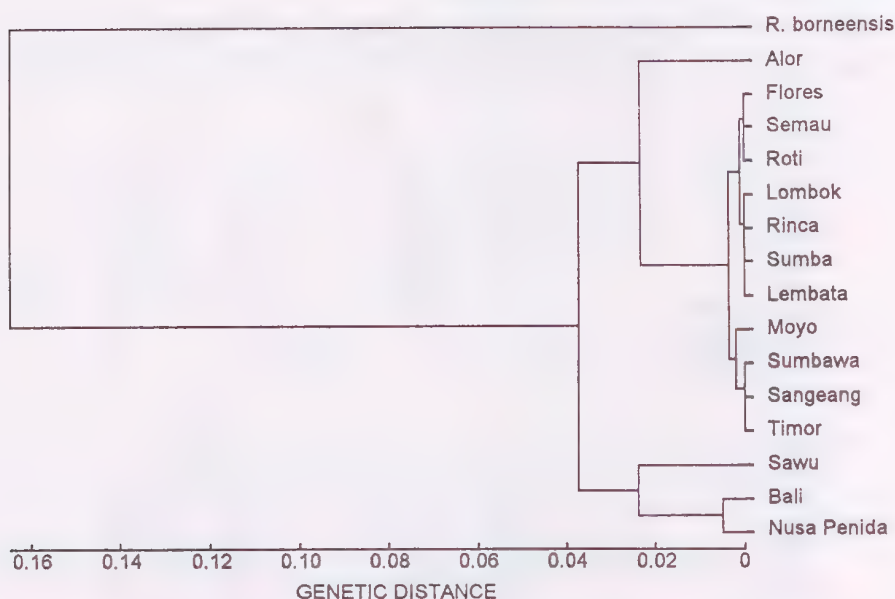


Figure 5 Dendrogram computed by UPGMA from the genetic distance (Nei standard distance, unbiased) between island populations of *Rhinolophus simplex* and *R. borneensis* from Java.

The characters loading most heavily (>0.6) on function 1 and presumed important discriminants between *R.s. simplex* and both *R. s. parvus* and *R.s. subsp. nov.* are snout to vent length, SV and vertical sella height, VSH (Table 5b). Characters loading most heavily on function 2 (>0.6) and presumed important discriminants between *R. s. parvus* and *R.s. subsp. nov.* are snout to vent length and pes length, PES (Table 5b).

GENETICS

The gene frequencies are presented in Table 6. Fifteen of the 30 loci scored showed variation within islands. The genotype frequencies for all occurrences of polymorphism within an island did not differ significantly from the Hardy-Weinberg expectations. Mean heterozygosity levels are presented at the bottom of Table 6. They fall within the usual range observed for mammalian populations (Nevo, Beiles and Ben-Shlomo 1984).

Much of the variation within *Rhinolophus simplex* was due to inter-island differences. *F*-statistics revealed four loci that had F_{ST} greater than 0.1. These were *Acon-2* (0.83), *Idh-2* (0.63), *Pep-D* (0.16) and *6PgD* (0.22). The mean F_{ST} over all loci was 0.42 with bootstrapped 95% confidence limits of 0.09 and 0.67. However, for most loci, there was little or no variability within or between islands and the unbiased Nei genetic distances between islands was low, being generally less than 0.04 (Table 7). These distances, together with those estimated from a sample of 18 individuals of *R. borneensis*

from Java were subjected to cluster analysis and the resultant dendrogram is presented in Figure 5. This dendrogram reveals the integrity of *R. simplex* as a species distinct from *R. borneensis*.

SYSTEMATICS

Rhinolophus simplex simplex Andersen, 1905

Rhinolophus simplex Andersen, K., 1905: 76, Pl. 3.

Holotype

British Museum No. 97.4.18.4, adult female, in alcohol, collected June 1896 by A. Everett.

Type locality

Lombok I., Nusa Tenggara, altitude 2500 ft (ca. 830 m).

Diagnosis

Rhinolophus s. simplex differs from both *R. simplex parvus* and *R. simplex subsp. nov.* in averaging larger in all skull, dental and dentary measurements, except for the posterior width of the sphenoid/pterygoid bridge; SW, and external measurements, except pes length, PES, and basal sella length, BSL, (Tables 1a, b). It differs almost absolutely from *R.s. subsp. nov.* in tibia length and forearm length (see Table 1). I_1M_3 longer relative to outside cochleae width, nasal inflation breadth, C^1M^3 length and outer M^3M^3 width (Figures 6, 7a, b, c, respectively). It differs from *R.s. parvus* in having snout to vent length longer relative to pes

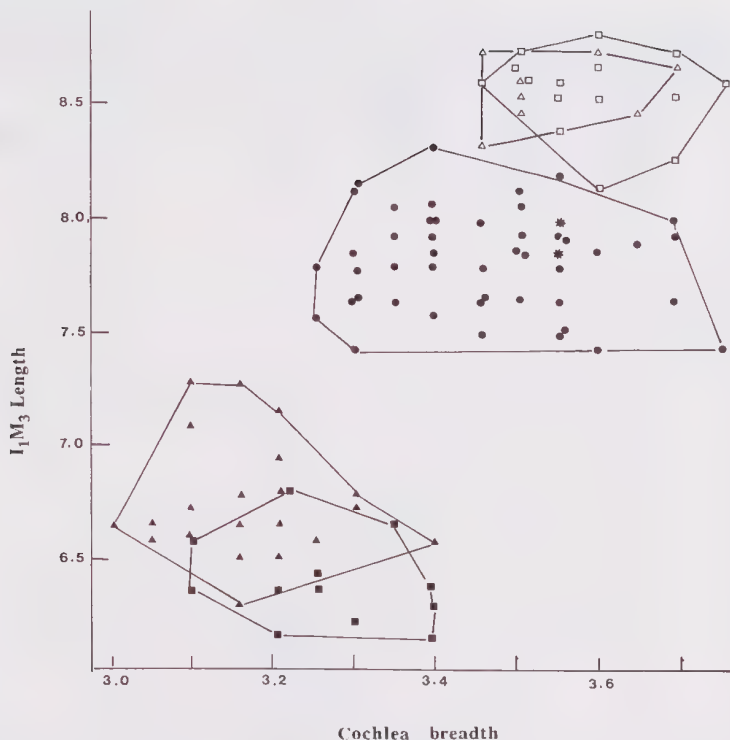


Figure 6 Plot of lower tooth row length, I_1M_3 , versus cochlea breadth, CW, for *Rhinolophus simplex* subspecies, *R. megaphyllus* (\square) and *R. borneensis importunus*. Other taxon symbols as for Figure 1.

length (Figure 8).

It is approximately the same size as *R. s. keyensis*. For example: greatest skull length 17.66 (16.75–18.45) *v.* 17.63 (17.50–17.25), zygomatic width 8.73 (8.05–9.15) *v.* 8.78 (8.65–8.90) and forearm length 41.9 (39.0–44.9) *v.* 41.4 (41.4–41.5)]. It differs from *keyensis* in having a smaller sella, with vertical sella height absolutely shorter 3.9 (3.2–4.3) *v.* 4.5 (4.5–4.5) and vertical sella breadth averaging narrower 2.0 (1.7–2.4) *v.* 2.4 (2.1–2.7).

Description

Skull and dentition

Rhinolophus s. simplex is larger than *R. s. parvus* and *R. s. subsp. nov.* (Table 1). Specimens show some variation in overall size and shape, but most of this variation may be found in a single population, for example, Moyo I. This can be appreciated by the wide distribution of the values for Moyo I. for the functions 1 and 2 scores from the DFA within the *R. s. simplex* cluster (Figure 4a). This is also true for those characters that were not quantified such as the size and shape of the anterior rostral swellings and the juxtaposition of the upper and lower vestigial premolar with the other premolars.

The junction of the supraorbital ridges is usually behind the mid-point of the orbital cavity but occasionally it is anterior to that point. The median anterior rostral swellings also vary considerably in size and extent of inflation in relation to the supraorbital length (Figure 9); some individuals, from throughout the range of *R. s. simplex* approximate the large size and inflation of the two individuals of *R. s. keyensis* from the eastern Kai Kecil I. The size and extent of crowding of the vestigial upper and lower premolar was extremely variable. Usually the anterior upper premolar was in contact with the canine but its contact with the posterior premolar was extremely variable. The lower vestigial premolar varied from being located almost in the tooth row between the anterior and posterior premolar, sometimes not in solid contact with these adjacent premolars, to being totally extruded such that the anterior and posterior premolars are in contact.

The anterior basisphenoid has a marked depression or pit which is much lower than the surface of the basioccipital. This is quite different from the shape of this region in *R. megaphyllus ignifer* where the basioccipital surface runs smoothly into a shallow basisphenoid groove.

The posterior palate margin terminates at M^2 mid

Table 6 Allele frequencies, mean heterozygosity and sample sizes in island populations of *Rhinolophus simplex* and *R. borneensis* from Java. A dash indicates the allele was not detected. The mean heterozygosity and its standard error, and mean number individuals (N) per locus are shown at the bottom of the table. No variation was detected at the following loci: *Acon-1*, *Enol*, *Fdp*, *Fum*, *Gapd*, *G6pd*, *Got-1*, *Gp-1*, *ldh-1*, *ldh-2*, *Mdh-1*, *Mdh-2*, *Np* and *Pep-C1*.

LOCUS	GENE	ISLAND						
		BALI	N.PENIDA	LOMBOK	SUMBAWA	MOYO	SANGEANG	RINCA
<i>Acon-2</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	—	—	—
	C	—	—	1.00	1.00	1.00	1.00	1.00
	D	1.00	1.00	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Ada</i>	A	—	—	—	—	—	—	—
	B	—	—	—	0.10	—	—	—
	C	1.00	1.00	1.00	0.90	1.00	1.00	1.00
	D	—	—	—	—	—	—	—
<i>Dia</i>	A	—	—	—	0.10	0.05	—	—
	B	1.00	1.00	1.00	0.90	0.95	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Gda</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	—	—	—
	C	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>áGpd</i>	A	—	—	—	—	—	—	0.12
	B	—	—	—	—	—	—	—
	C	1.00	1.00	1.00	1.00	1.00	1.00	0.88
<i>Got-2</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
<i>ldh-2</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
<i>Ldh-1</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	0.88
	B	—	—	—	—	—	—	0.12
<i>Mpi</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	—	—	—	—	—	—	—
<i>Pep-A</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
<i>Pep-B</i>	A	—	—	—	—	0.05	—	—
	B	—	—	—	0.10	0.05	—	—
	C	—	—	—	—	—	—	—
	D	1.00	1.00	1.00	0.80	0.90	1.00	1.00
	E	—	—	—	—	—	—	—
	F	—	—	—	0.10	—	—	—
<i>Pep-D</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	0.30	—	—
	C	1.00	1.00	1.00	0.80	0.60	1.00	1.00
	D	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
	F	—	—	—	0.20	0.10	—	—
	G	—	—	—	—	—	—	—
<i>6Pgđ</i>	A	0.44	0.07	0.25	0.50	0.50	0.50	0.12
	B	0.50	0.93	0.75	0.50	0.50	0.50	0.88
	C	—	—	—	—	—	—	—
	D	0.06	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Pgm</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	—	—	—	—	—	—	—
<i>Sod</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mean Heterozygosity		0.019	0.005	0.017	0.056	0.046	0.033	0.025
Standard error		0.019	0.005	0.017	0.025	0.026	0.033	0.014
N per locus		9	7	2	5	10	1	4

Table 6 (continued)

SUMBA	FLORES	LEMBATA	ALOR	ISLAND TIMOR	SEMAU	ROTI	SAVU	JAVA
—	—	—	—	—	—	0.04	—	1.00
—	—	—	—	—	0.12	—	—	—
1.00	1.00	1.00	1.00	1.00	0.88	0.96	—	—
—	—	—	—	—	—	—	0.25	—
—	—	—	—	—	—	—	0.75	—
—	—	—	—	—	—	—	—	0.08
—	—	—	—	—	—	—	—	0.17
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.50
—	—	—	—	—	—	—	—	0.25
—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	0.96	0.80	0.36
—	—	—	—	—	—	—	—	0.64
—	—	—	—	—	—	0.04	—	—
—	—	—	—	—	—	—	0.20	—
—	—	—	0.04	—	—	—	—	—
—	—	—	—	—	—	—	—	1.00
1.00	1.00	1.00	0.96	1.00	1.00	1.00	1.00	—
—	—	0.17	0.05	—	—	—	—	—
—	—	—	—	—	—	—	—	0.97
1.00	1.00	0.83	0.96	1.00	1.00	1.00	1.00	0.03
—	—	—	0.04	—	—	—	—	—
—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.96	1.00	1.00	1.00	0.92	0.94
—	—	—	—	—	—	—	0.08	—
—	—	—	—	—	—	—	—	0.06
—	0.25	0.33	0.73	—	—	—	—	—
—	0.75	0.67	0.23	1.00	1.00	1.00	1.00	1.00
—	—	—	0.04	—	—	—	—	—
—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	0.86	1.00	1.00	0.96	0.98	0.75
—	—	—	0.14	—	—	0.04	0.02	0.25
—	—	—	0.04	—	—	—	0.02	—
0.92	1.00	0.83	0.96	1.00	1.00	1.00	0.98	0.09
—	—	—	—	—	—	—	—	0.03
0.08	—	0.17	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	0.94
1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	—
—	—	—	—	—	—	—	—	0.06
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
0.08	—	—	—	—	0.17	—	—	—
—	—	—	—	—	—	—	—	—
0.92	0.75	1.00	0.46	0.92	0.66	0.73	1.00	1.00
—	—	—	0.09	—	—	—	—	—
—	—	—	0.09	—	—	—	—	—
—	0.25	—	0.27	0.08	0.17	0.27	—	—
—	—	—	0.09	—	—	—	—	—
—	—	—	—	—	—	—	—	—
0.08	0.25	0.17	—	0.42	0.25	—	—	—
0.84	0.75	0.83	1.00	0.58	0.75	1.00	1.00	0.94
0.08	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	0.06
—	—	—	—	—	—	—	—	—
1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	0.97
—	—	—	—	—	—	—	0.02	0.03
—	—	—	—	—	—	—	—	—
—	—	—	—	—	0.12	—	—	—
1.00	1.00	1.00	1.00	1.00	0.88	1.00	1.00	1.00
0.022	0.050	0.051	0.059	0.023	0.051	0.023	0.034	0.073
0.013	0.028	0.025	0.029	0.018	0.026	0.014	0.017	0.029
6	2	3	11	6	4	11	20	18

Table 6 Allele frequencies, mean heterozygosity and sample sizes in island populations of *Rhinolophus simplex* and *R. borneensis* from Java. A dash indicates the allele was not detected. The mean heterozygosity and its standard error, and mean number of individuals (N) per locus are shown at the bottom of the table. No variation was detected at the following loci: *Acon-1*, *Ca*, *Enol*, *Fdp*, *Fum*, *Gapd*, *G6pd*, *Got-1*, *Gp-1*, *Idh-1*, *Idh-2*, *Mdh-1*, *Mdh-2*, *Np* and *Pep-C1*.

LOCUS	GENE	ISLAND						
		BALI	N.PENIDA	LOMBOK	SUMBAWA	MOYO	SANGEANG	RINCA
<i>Acon-2</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	—	—	—
	C	—	—	1.00	1.00	1.00	1.00	1.00
	D	1.00	1.00	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Ada</i>	A	—	—	—	—	—	—	—
	B	—	—	—	0.10	—	—	—
	C	1.00	1.00	1.00	0.90	1.00	1.00	1.00
	D	—	—	—	—	—	—	—
<i>Dia</i>	A	—	—	—	0.10	0.05	—	—
	B	1.00	1.00	1.00	0.90	0.95	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Gda</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	—	—	—
	C	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>δGpd</i>	A	—	—	—	—	—	—	0.12
	B	—	—	—	—	—	—	—
	C	1.00	1.00	1.00	1.00	1.00	1.00	0.88
<i>Got-2</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
<i>Idh-2</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
<i>Ldh-1</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	0.88
	B	—	—	—	—	—	—	0.12
<i>Mpi</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	—	—	—	—	—	—	—
<i>Pep-A</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	C	—	—	—	—	—	—	—
	D	—	—	—	—	—	—	—
<i>Pep-B</i>	A	—	—	—	—	0.05	—	—
	B	—	—	—	0.10	0.05	—	—
	C	—	—	—	—	—	—	—
	D	1.00	1.00	1.00	0.80	0.90	1.00	1.00
	E	—	—	—	—	—	—	—
	F	—	—	—	0.10	—	—	—
<i>Pep-D</i>	A	—	—	—	—	—	—	—
	B	—	—	—	—	0.30	—	—
	C	1.00	1.00	1.00	0.80	0.60	1.00	1.00
	D	—	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
	F	—	—	—	0.20	0.10	—	—
	G	—	—	—	—	—	—	—
<i>6Pgd</i>	A	0.44	0.07	0.25	0.50	0.50	0.50	0.12
	B	0.50	0.93	0.75	0.50	0.50	0.50	0.88
	C	—	—	—	—	—	—	—
	D	0.06	—	—	—	—	—	—
	E	—	—	—	—	—	—	—
<i>Pgm</i>	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	—	—	—	—	—	—	—
<i>Sod</i>	A	—	—	—	—	—	—	—
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mean Heterozygosity		0.019	0.005	0.017	0.056	0.046	0.033	0.025
Standard error		0.019	0.005	0.017	0.025	0.026	0.033	0.014
N per locus		9	7	2	5	10	1	4

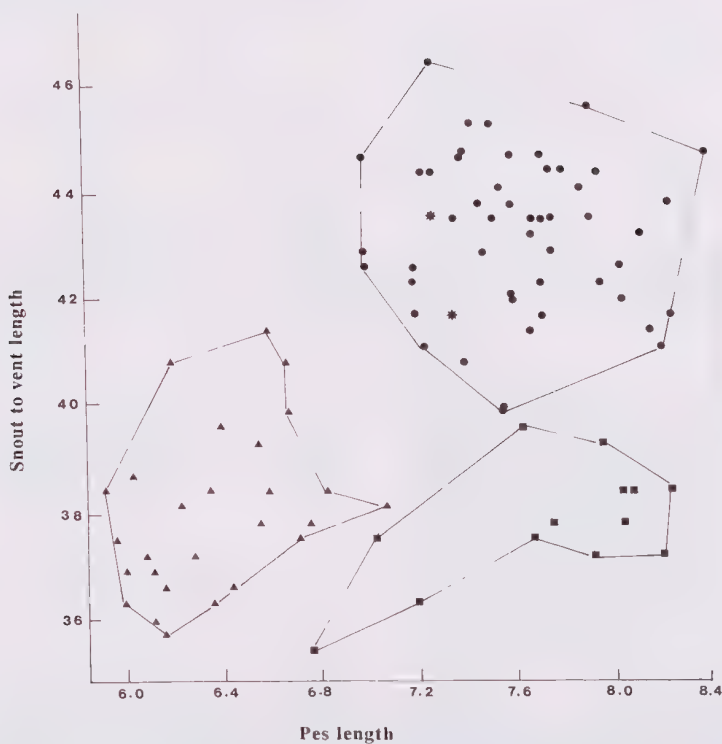


Figure 8 Plot of snout to vent length *versus* pes length for subspecies of *R. simplex*. Subspecies codes as for Figure 1.

Diagnosis

Rhinolophus s. keyensis differs from *R. s. simplex* as diagnosed earlier for this subspecies.

It differs from *R. s. parvus* in averaging larger in all skull, dentary and most external characters (see Table 1). With the following characters it is absolutely larger: ear length, forearm length, maximum anterior noseleaf breadth, basal sella length, vertical sella height, vertical sella breadth, greatest skull length, rostrum length and M¹ width (see Table 1).

It differs from *R. s. amiri* subsp. nov. in averaging larger in most skull, dentary, dental and external characters (see Table 1). With a number of characters it is absolutely larger, for example: forearm length, vertical sella height, greatest skull length, zygomatic width, cranial width and C¹M³ length (see Table 1).

Description

Apart from differences described in the diagnosis of *R. s. simplex*, *R. s. keyensis* is very similar to that species. In the two specimens of *R. s. keyensis* available to us, the juncture of the supraorbital ridge is just posterior to the orbital cavity mid point, supraorbital length greater than nasal inflation breadth (Figure 9); median anterior rostral swellings inflated; anterior upper premolar in contact with both canine and posterior premolar;

lower vestigial premolar extruded from toothrow but still in contact with adjacent premolars – in WAM 42642 the anterior and posterior premolars are not in contact, whereas in WAM M42643 they are in solid contact.

The form of the basiphenaoid, palate and dentition is similar to *R. s. simplex*.

Externals

The external characters similar to *R. s. simplex* but anterior noseleaf wider (9.2 *v.* 8.1). The vertical sella taller (4.5 *v.* 3.9) and wider (2.4 *v.* 2.0) with a slightly wider mid part than *R. s. simplex*, smoothly rounded at apex.

Pelage and skin colour and baculum

As described for *R. s. simplex*.

Distribution

Kai Kecil I.

Remarks

This form is only weakly separated from *R. s. simplex*; the subspecific distinction resting solely on the shape and size of its sella. In all other characters it appears to be very close to *R. s. simplex*, as attested to by its closeness to that subspecies in discriminant function space (Figures

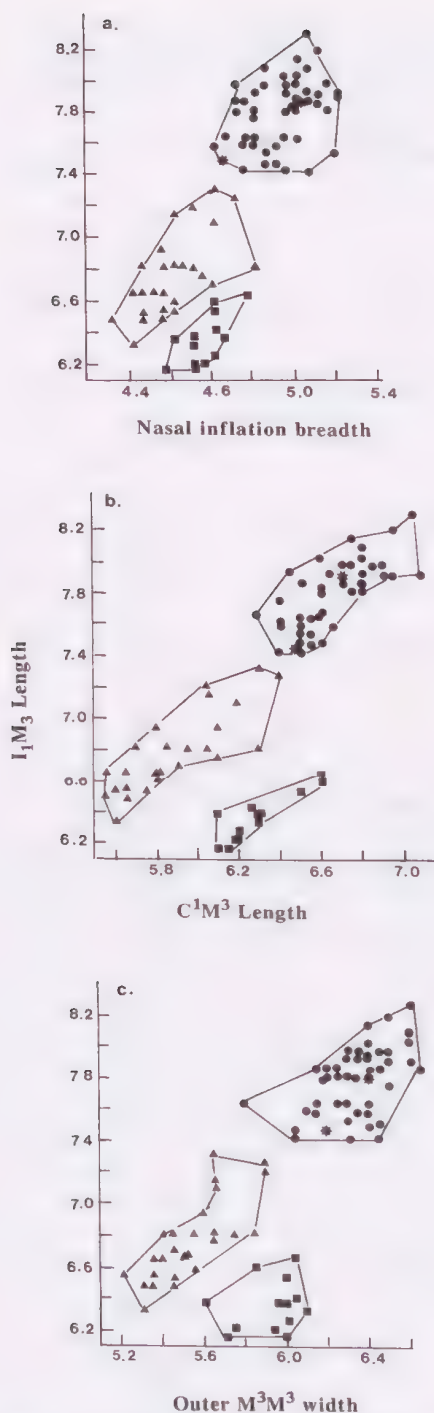


Figure 7 Plot of lower tooth row length, I_1M_3 , versus (a) nasal inflation breadth, NIB; (b) upper maxillary tooth row length, C^1M^3 ; and (c) outer M^3M^3 width, M^3M^3W ; for subspecies of *Rhinolophus simplex*; subspecies symbols as for Figure 1, caption.

point; occasionally there is a slight median postpalatal protuberance but more usually this is a smooth U shape; premaxilla posteriorly terminates at P^3 mid point; sphenoidal/pterygoid bridge obscures anterior sphenorbital fissure when viewed from the ventral aspect; incisors weak, bilobed; M^{1-2} hypocone well developed.

Externals

The external characters are similar to those described by Andersen (1905) for *Rhinolophus simplex*. The anterior noseleaf is moderately wide (8.2) with an obvious anteromedian notch. The vertical sella is longer than the basal sella (4.0 v. 2.3), smoothly curved at the apex and not noticeably constricted. Ears are moderately long (17.8), outer apical margin reasonably concave.

Pelage and skin colour

Dorsal pelage of most specimens Fuscous, which is colour of distal one-third of hairs, the basal part of which is Drab. Ventral surface pure Drab.

Occasional specimens of both sex paler, with dorsal surface Russet, which is colour of distal one-third of hairs, the basal part of which is Cream Color. Ventral surface pure Fawn Color. Wing and ears Fuscous.

Baculum

The shape of bacula among *Rhinolophus simplex* largely differs in the extent of the incision in the posteroventral basal margin (Figure 10, Table 8), which ranges from deeply incised in WAM M38252 (Bali I). to slightly concave in WAM M30249 (Sumba I). All these basal types occur in *R. s simplex*.

Distribution

Many islands in the Inner Banda Arc: Bali, Nusa Penida, Lombok, Sumbawa, Moyo, Sangeang, Komodo, Rinca, Flores, Lembata, Alor, Wetar islands and Sumba Island in the outer Banda Arc. Its ability to occupy new habitats, such as defence tunnels build by Japanese during the Second World War, suggest that it is a good colonist and that it probably exists on many other islands in this region.

Rhinolophus simplex keyensis Peters, 1871

Rhinolophus megaphyllus keyensis Peters, W., 1871.

Types

Cotypes, Mus. Berol. No. 3240 and No. 3291.

Type locality

Key-Inseln (= Kai Islands).

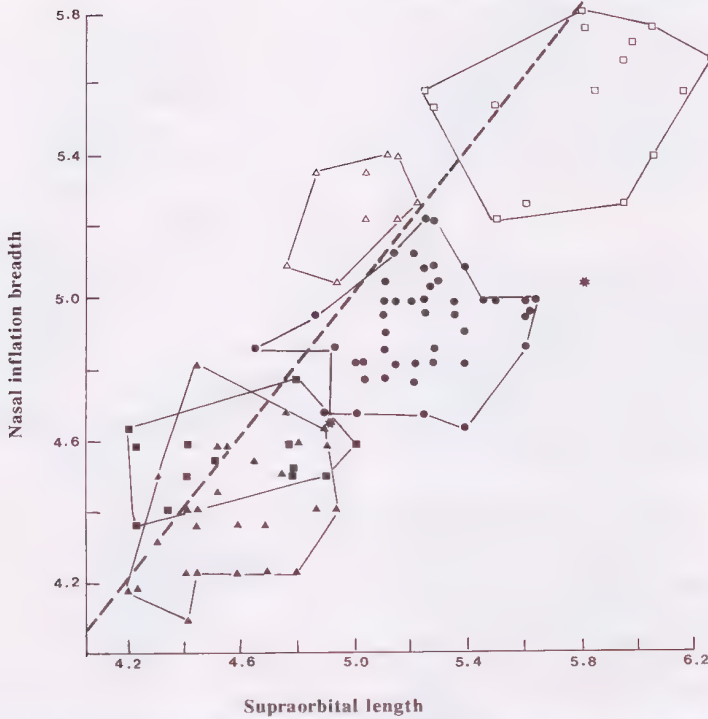


Figure 9 Plot of nasal inflation breadth, NIB, versus supraorbital length, NIL, for the taxa *Rhinolophus simplex simplex*, *R. s. parvus*, *R. s. subsp. nov.* *R. megaphyllus* (□) and *R. borneensis parvus*. The oblique broken line joins values where NIB = NIL. Other taxon symbols as for Figure 1, caption. Following Hill (1992), those forms with values generally below the line should be *R. megaphyllus* while those generally above the line are other species in the 'ferrumequinum' group.

4a, b). Future collections from Tanimbar and Wetar Is may help clarify its taxonomic status with respect to *R. s. simplex*.

Rhinolophus simplex parvus Goodwin, 1979

Rhinolophus borneensis parvus Goodwin, 1979: 102-105.

Holotype

American Museum, Natural History No. 237766, adult male, skin and skull, collected 27 March 1968.

Type locality

Lia Hoo Cave, nr Fatu Maca village, 11 km S Baucau, Timor, altitude ca. 550 m.

Diagnosis

Rhinolophus simplex parvus differs from *Rhinolophus s. simplex* and *R. s. keyensis* as diagnosed earlier for these subspecies.

Differs from *Rhinolophus simplex subsp. nov.* in averaging larger (but with measurements overlapping) in all skull and dentary characters except supraorbital length and lower tooth row

length (Table 1a). Also the relationship between lower tooth row length and : nasal inflation breadth, C¹M³ length and outer M³M³ width differs (Figures 7a,b,c). General body measurements also average larger except those related to facial foliations: maximum noseleaf breadth, basal sella length, vertical sella height, maximum vertical sella breadth.

Description

Apart from differences described in the diagnoses of *R. s. simplex*, *R. s. parvus* is very similar to that subspecies. The skull, however, tends to have the juncture of supraorbital and lambdoidal ridges level with orbital cavity mid point (36%), just posterior (36%) or well posterior from that point (28%); anterior sphenoid/pterygoid bridge tends to obscure more of sphenorbital sinus when viewed from ventral aspect.

Pelage and skin colour also differs slightly. Dorsal pelage Cinnamon Brown, which is colour of distal one-third of hairs, basal part of which is Drab. Ventral surface pure Fawn Color. Wings Grayish Brown, Ears Fawn Color.

Table 7 Nei's unbiased genetic distance between *Rhinolophus simplex* populations and *R. borneensis* from Java.

NUSA PENIDA	0.005						
LOMBOK	0.034	0.033					
SUMBAWA	0.035	0.041	0.000				
MOYO	0.038	0.045	0.004	0.000			
SANGEANG	0.034	0.041	0.000	0.000	0.004		
RINCA	0.038	0.034	0.000	0.004	0.008	0.004	
SUMBA	0.038	0.034	0.000	0.004	0.007	0.005	0.000
FLORES	0.034	0.033	0.000	0.000	0.000	0.000	0.000
LEMBATA	0.039	0.036	0.000	0.005	0.009	0.005	0.000
ALOR	0.070	0.062	0.026	0.030	0.031	0.035	0.026
TIMOR	0.033	0.038	0.000	0.000	0.002	0.000	0.002
SEMAU	0.032	0.031	0.000	0.000	0.001	0.002	0.000
ROTI	0.043	0.035	0.002	0.007	0.010	0.011	0.002
SAVU	0.028	0.020	0.029	0.038	0.042	0.038	0.030
JAVA	0.171	0.161	0.162	0.163	0.174	0.172	0.159
	BALI	NUSA P.	LOMBOK	SUMBAWA	MOYO	SANGEANG	RINCA

R. megaphyllus whereas the narrower cranium and nasal swellings and overall small size of *R. nanus* are more suggestive of *R. simplex*. However, J.E. Hill (pers. comm.) informed us that the holotype of *R. nanus* is very old and has a damaged skull. Consequently, he considers that the narrowing of the skull of *R. nanus* may well be an artefact because otherwise the skull is very like that of *R. truncatus*.

Hill (1992:100) separated the *R. megaphyllus* species complex (in which he includes *R. s. simplex* and *R. s. keyensis*) from other IndoMalayan species in the *ferrumequinum* group principally on the supraorbital crests combining at a point behind the centre of the orbital cavity; such that the supraorbital length (from junction of crests to nares) is much greater than rather than slightly greater than or equal to the width across the anterior lateral rostral swellings (in our terminology NIL NIB) and the supraorbital depression being larger than it is wide. The association by Goodwin (1979) and Hill (1992) of the form *parvus* with *R. borneensis* and *R. celebensis*, respectively, depended largely on the supraorbital crests of *parvus* merging anterior to the mid point of the orbital cavity. However, in the sample of *parvus* available to us this junction point was variable; sometimes it was level with the point, or just behind or well behind it (an *R. simplex* character). Also the supraorbital length is frequently much greater than the width across the outer lateral rostral swellings (see also Figure 9). Clearly in the form *parvus* (and *amiri*) this latter character is too variable for it to be usefully diagnostic in terms of the association of *parvus*, although it appears to hold true for *R. borneensis* and generally so for *R. megaphyllus* and *R. s. simplex*. Goodwin (1979:104) further considered that *R. simplex* differed from *parvus* in being larger

overall and in having "dentition (that) is somewhat more primitive. The vestigial premolars in both upper and lower jaws are generally not as crowded, but there is some individual variation in this condition" Further, "the sella of *simplex* is slightly constricted and the connecting process is not as prominent". In the specimens available to us there was considerable variation in the extent of crowding in both the upper and lower vestigial premolar, particularly the lower. The lower premolar in both *parvus* and *R. s. simplex* varied in its position from almost being in the toothrow to being completely extruded such that this first and second premolars were in contact. Further we can find no consistent difference between *parvus* and *R. s. simplex* in the shape of either the sella or the connecting process.

We associate the form *parvus* with *R. simplex* rather than with *R. borneensis*, as suggested by Goodwin (1979) or with *R. celebensis* as considered by Hill (1992). This is because of its morphological closeness to *R. simplex* and because, as discussed above, the characters used by these authors to diagnose it from *R. simplex* cannot be substantiated by us. It is also relevant here that our electrophoretic study, using 30 loci, concluded that there was little or no detectable genetic difference between *R. s. simplex*, *R. s. parvus* and *R. s. amiri*. For example the population of *R. s. parvus* (Timor) is not genetically differentiated from several *R. s. simplex* populations (Sangeang, Sumbawa), while two populations of *R. s. amiri* (Roti and Semau) are closer genetically to the majority of the *R. s. simplex* populations than they are to the third population of *R. s. amiri* (Savu). The significance of the apparent clusters within *R. simplex* based on the Nei genetic distance metric is tenuous because it is the product of gene frequency variation at just one or two loci. Thus Alor differentiates due to

Table 7 (continued)

0.000							
0.000	0.000						
0.025	0.006	0.010					
0.002	0.000	0.003	0.029				
0.000	0.000	0.002	0.021	0.000			
0.002	0.000	0.004	0.020	0.006	0.000		
0.030	0.030	0.032	0.057	0.035	0.028	0.030	
0.157	0.166	0.150	0.193	0.169	0.164	0.160	0.151
SUMBA	FLORES	LEMBATA	ALOR	TIMOR	SEMAU	ROTI	SAVU

variability at two loci, *Idh-2* and *Pep-D*, while the Bali-Nusa Penida-Savu cluster is largely due to *Acon-2* allele frequency differences.

Hill (1983) considered that the form *parvus* was very similar to *R. madurensis* Andersen, 1918 from Madura I., a view supported by Bergmans and van Bree (1986) who considered *parvus* synonymous with *R. celebensis madurensis*. We have been unable to examine specimens of the form *madurensis*, but if

parvus is indeed synonymous with *R. celebensis*, then it brings into question the distinction between other species in the *ferrumequinum* group (*sensu* Tate and Archbold 1939).

We have not examined in depth the taxonomic relationships between all the forms of *R. megaphyllus* (*sensu* Hill, 1992). Our conclusions, then, with respect to the specific status of the forms, *R. simplex* (*simplex*, *keyensis*, *parvus* and

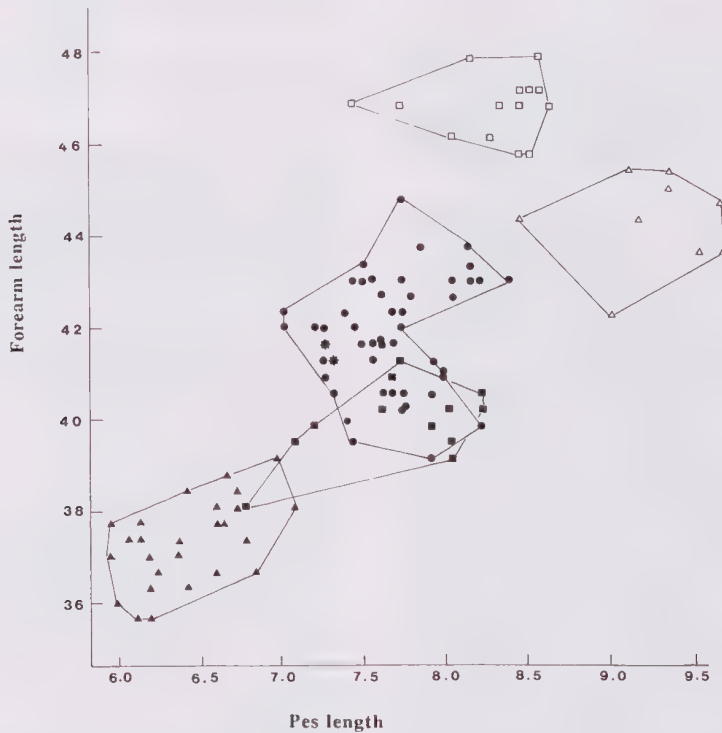


Figure 11 Plot of forearm length versus pes length for *R. simplex* subspecies, *R. megaphyllus* (□) and *R. borneensis*. Other taxa codes as for Figure 1.

Table 8 Mean and range, in mm, and sample size of baculum: greatest length, basal height and basal breadth, for *Rhinolophus simplex* subspecies and *R. megaphyllus*.

	Greatest Length	Basal Height	Basal Breadth	N
<i>R. s. simplex</i>	3.00 (2.67–3.48)	0.85 (0.67–0.99)	0.84 (0.60–0.95)	11
<i>R. s. parvus</i>	2.98 (2.48–3.32)	0.77 (0.76–0.94)	0.78 (0.63–0.97)	3
<i>R. s. amiri</i> subsp. nov.	2.66 (2.64–2.68)	0.74 (0.67–0.85)	0.74 (0.67–0.83)	4
<i>R. megaphyllus</i>	2.70 (2.68–2.72)	0.82 (0.82–0.82)	0.83 (0.78–0.88)	2

amiri), are tentative. Clearly these four forms differ from *R. megaphyllus ignifer* in general size, aspects of the basicranium and shape of basal part of baculum and for *parvus* and *amiri* also in the shape of the rostrum. Some independent support for this decision comes from an electrophoretic study incorporating liver tissue from specimens used in this paper, which shows that Queensland *R. megaphyllus* differs at 17 percent of their electrophoretic loci, including 4 fixed differences, from *R. simplex* (T. Reardon pers. comm.) However, for a complete appraisal of the relationship of these forms with *R. megaphyllus* it would be necessary to compare them in detail with *R. m. megaphyllus* and the smaller forms (*R. m. vandeuseni*) from the islands off northeast New Guinea. These smaller forms of *R. megaphyllus*, which appear to be connected to *R. megaphyllus ignifer* by intermediates (Koopman 1982), are approximately the same size as *R. s. simplex* (see Koopman 1982).

The taxonomic status of the Maluku form *R. annectens* (Wetar I.) is indeterminate. This form is known only from the holotype which we were unable to examine. However, this holotype was examined by J.E. Hill (pers. comm.) who stated that it is a smashed skull, which on size could be *parvus*, or close to it.

Prior to our study, *Rhinolophus simplex* was reported only from Lombok, Sumbawa and Komodo islands, (as *R. s. simplex*); Kai (as *R. s. keyensis*) and Timor (as *R. celebensis parvus*). We have recorded it additionally from Bali, Nusa Penida, Moyo, Sangeang, Rinca, Flores, Lembata, Alor, Sumba, Savu, Roti and Semau. Frequently on these islands it was collected from tunnels built by the Japanese during the Second World War. It was often the only species present in such tunnels.

The occurrence of morphological variation among *Rhinolophus simplex* from some of the Gondwanic islands of the outer Banda Arc (Sumba, Savu, Roti, Semau, Timor and Kai Kecil) reflects similar variation in the microchiropterans *Hipposideros sumbae* and *Taphozous aches* that have been examined from this region (Kitchener and Maryanto 1993; Kitchener *et al.* 1993). The presence on Semau of *R. s. amiri*, a population separated by a narrow water gap of only about three kilometres from *R. s. parvus* on Timor, suggests reduced gene

flow is probably operating between these two populations to maintain these morphological distinctions.

SPECIMENS EXAMINED

Rhinolophus borneensis importunus

INDONESIA

Java I: Kiskenda, 7°6'S, 110°16'E, WAM (M39310–13, M39319–21, M39328, M39354–5, M39361–2, M39367, M39380) (10♂, 4♀).

Rhinolophus megaphyllus ignifer

AUSTRALIA

Queensland: McIlwraith Range, 13°47'S, 142°15'E, WAM M29972 (1♂); Iron Range, 11°37'S, 142°55'E, WAM M29977–86, (6♂♂, 4♀♀); Chillagoe, 17°9'S, 144°31'E, WAM M29973 (1♀); Yarramulla Lava Tunnels, 18°13'30"S, 144°40'30"E, WAM M29974–6 (3♀♀).

Rhinolophus simplex amiri subsp. nov. (paratypes)

INDONESIA

Savu I: Desa Menia, 10°29'S, 121°55'E, WAM (M35113, M35117–8, M35120–25, M35127, M35129, M35132–8, M35222, 35260–2) (8♂♂, 15♀♀).

Roti I: Baa, 10°44'S, 123°6'E, WAM (M35351–2, M35370–4, M35376–8, M35380, M35389, M35391–3 (7♂♂, 8♀♀); Sanggoen, 10°43'S, 123°9'E, WAM M35422–3 (2♂♂).

Semau I: Uiasa, 10°10'S, 123°28'E, WAM (M35599, M35604, M35606 (1♂, 2♀♀); Onansila, 10°13'S, 123°30'E, WAM M38014 (1♂).

Rhinolophus simplex parvus

INDONESIA

Timor I: Baumata, 10°11'S, 123°43'E, WAM (M30059, M30096–7, M30123, M30125–6, M30128–40, M30145–7, M30150–2, M30155–7, WAM 30160–2, M30172) (5♂♂, 27♀♀); Panite, 9°50'S, 124°29'E, WAM (M34896, M34897–9, M34960, M34962, M34969–72, M35009) (2♂♂, 10♀♀).

Rhinolophus simplex simplex

INDONESIA

Bali I.: Candi Kuning, 8°7'S, 115°9'E, WAM 38441

(1♀); Payongan 8°29'E, 115°15'E, WAM M38424 (1♀); Ubud, 8°30'S, 115°16'E, WAM (M38372, M38409) (1♂, 1♀); Gianyar, 8°23'S, 115°23'E, WAM (M38252-3, M38263, M38265, M38268, M38270, M38273) (3♂♂, 4♀♀).

Nusa Penida I: Sampalan, 8°41'S, 115°34'E, WAM (M39580-1, M39584) (3♀♀).

Lombok I: Ngali, 8°55'S, 116°17'E, WAM (M31111, M33860-4) (2♂♂, 4♀♀).

Sumbawa I: Desa Belo, 8°52'S, 116°50'E, WAM (M31336-7) (1♂, 1♀); Desa Sangeang, 8°18'S, 118°56'E, WAM (M31601-4, M31619) (1♂, 4♀).

Moyo I: Brang Kua, 8°14'15"S, 117°36'45"E, WAM (M31912-5, M31921) (3♂♂, 2♀); Tanjung Pasir, 8°23'15"S, 117°31'30"E, WAM (M31952-3, WAM M31962-4, M31966, M31968-79) (7♂♂, 12♀♀).

Sangeang I: 8°13'30"S, 119°00'20"E, WAM M31588 (1♂).

Rinca I: 8°39'S, 119°40'E, WAM (M32930-2, M32937-9) (6♂♂).

Flores I: Daraloeng Baru, 8°33'S, 122°39'E, WAM (M32589-90, M32597-8) (2♂♂, 2♀♀).

Alor I: Kalahabi, 8°14'S, 124°32'E, WAM (M37615-7, M37651-2, M37654) (1♂, 5♀♀).

Lembata I: Kampung Merdeka, 8°22'S, 123°31'E, WAM M32286 (1♀); Desa Boto, 8°31'S, 123°23'E, WAM M32429-30 (2♂♂).

Sumba I: Waingapu, 9°37'S, 120°14'E, WAM (M30249-50, M30252-3) (3♂♂, 1♀). Bondokodi 9°35'S, 119°8'E, WAM (M30486, M30492) (2♂♂).

Rhinolophus simplex keyensis

Kai Kecil I: Tual, 5°38'S, 132°44'E, WAM (M42642-3) (1♂, 1♀).

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of Mr J. Bannister, Director, Western Australian Museum during this research (now retired); and Dr M. Amir, Director, Balitbang Zoologi (LIPI). The Directors of the Indonesian Department responsible for the conservation of wildlife in Nusa Tenggara (BKSDA), Ir. J. Mochtar (NTT) and Ir. P. Supriadi (NTB) and Maluku Tenggara, Ir. J. Rustandi, provided us with great assistance in the field, as did a number of their staff.

To our colleagues who participated in the field work, particularly Dr R.A. How and Mr R.E. Johnstone, Western Australian Museum; Bapak Boeady, Ir Maharadatunkamsi, and Ir I. Maryanto, Museum Zoologicum Bogoriense, we extend our thanks for their effort and companionship.

We are particularly grateful to Ms Sue Hisheh and Mr Paul Ottaviana for assistance with the protein electrophoresis.

Expedition costs were defrayed by grants to Dr D.J. Kitchener from: National Geographic Society, Washington; Australian National Parks and

Wildlife Service, Canberra, and The Mark Mitchell Trust, South Australia; and a grant to Drs L.H. Schmitt, D.J. Kitchener and R.A. How from the Australian Research Council, Canberra. Garuda Indonesia kindly defrayed freight costs of the expeditions.

Mrs N. Cooper, Western Australian Museum, ran the computer analyses. Mrs S. Dalton and Mrs Anne Nevin, Western Australian Museum, typed the manuscript.

We are particularly grateful to Mr J.E. Hill, The Natural History Museum, London, and Dr R.A. How, Western Australian Museum, who critically commented on an earlier draft of the MS.

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Manuscript received 18 August 1993; accepted 1 March 1994.

Food of the blind cave fishes of northwestern Australia

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Abstract – Cape Range peninsula, in the arid northwest of Western Australia, contains the only cavernicolous fishes in Australasia, both of which are considered as vulnerable or endangered. They are associated with a stygofauna considered to be of Tethyan origin. *Ophisternon candidum* (Mees, 1962) (Synbranchiformes: Synbranchidae) and *Milyeringa veritas* Whitley, 1945 (Perciformes: Eleotrididae) occur widely in underground waters and are endemic to the peninsula. The gut contents of existing collections were examined to elucidate their prey. Both species of troglobitic fish are opportunistic in their feeding, able to utilize occasional packets of energy entering the stygal realm.

Ophisternon candidum eats the specialised stygofauna of the region, including *Halosbaena tulki* (Poore and Humphreys, 1992) (Thermosbaenacea) and atyid shrimps (*Stygiocaris* spp.) and also feeds opportunistically on aquatic larvae living in the more open part of the subterranean system. The biogeographic affinities of *O. candidum* is in accord with that of its main prey. The gut contents constitute the only records of *Stygiocaris* and *Halosbaena* from Tantabiddy Well (C-26), the type locality of *O. candidum*. *M. veritas* primarily feeds opportunistically on invertebrates accidentally introduced into the aquatic system (mostly terrestrial isopods and cockroaches) but also feeds on the stygofauna.

INTRODUCTION

The Cape Range peninsula in the arid northwest of Australia is noted for its subterranean animals, both a terrestrial fauna with wet forest affinities (Humphreys 1993a, 1993b, 1993c, 1993d), and an aquatic fauna with Tethyan affinities (Humphreys 1993a, 1993d; Knott 1993). Amongst the latter are two species of blind cave fish, the Blind or Cave Gudgeon, *Milyeringa veritas* Whitley, 1945 (Perciformes: Eleotrididae) and the Blind Cave Eel, *Ophisternon candidum* (Mees, 1962) (Synbranchiformes: Synbranchidae). These two species of fish comprise the entire vertebrate troglobite fauna of Australasia. While other stygobiontic fish have been extensively researched (e.g. Wilkens 1988), nothing is known of the ecology of those inhabiting the Cape Range peninsula.

The Synbranchidae, or swamp eels, are widely distributed in tropical and sub-tropical regions. They exhibit marked habitat plasticity, being predominantly freshwater inhabitants but extending into brackish and estuarine waters; the same species may occupy a range of epigeal habitats from streams and lakes to swamps and marshes. Swamp and marsh dwellers often show amphibious or burrowing habits and many are capable of aerial respiration (Rosen and Greenwood 1976).

The genus *Ophisternon* has a disjunct distribution, being found in Australasia, Indo-Malaya, west Africa and some island and mainland areas of the Caribbean. While the diet of *O. candidum* has been unrecorded previously, synbranchids are recognized as nocturnal predators (Moyle and Cech 1982). Cavernicolous species, showing considerable atrophy of the eye tissue, occur on the Yucatan peninsula, Mexico (*O. infernale*) (Rosen and Greenwood 1976) and in Australia (*O. candidum*).

The Eleotrididae are widespread in tropical and subtropical shallow marine to fresh waters mainly in the Indo-Pacific region (Nelson 1984). The monotypic genus *Milyeringa* is endemic to the Cape Range peninsula but the phylogenetic relationships between members of the family Eleotrididae have not been established (see discussion in Knott 1993). *M. veritas* is cavernicolous, eyeless and translucent. This species has been considered to feed opportunistically upon detritus, algae and whatever animals, including insects, accidentally fall into the water (Allen 1989).

Their subterranean habitat restricts observation in life and hence very little is known about the biology of these fishes. Nonetheless, they have respectively been classified as rare and recommended for total protection, and vulnerable (Michaelis 1985); both fish species as well as two of

the prey species (*Stygiocaris* spp.) have been listed under Schedule One of the Wildlife Protection Act of Western Australia owing to their small geographic distribution, low populations and vulnerability of their habitat.

To establish basic biological data required for conservation purposes the gut contents of existing collections have been examined to elucidate their prey.

METHODS

The intestines were either dissected out and later examined by flushing the contents, or the flushing was conducted *in situ* on intestines longitudinally incised. The contents were identified to whatever level practicable depending on the state of digestion. As no details are available of the treatment of the specimens prior to preservation, no attempt is made to quantify feeding rates.

With the exception of the holotype the gut contents were examined of all available specimens of *Ophisternon candidum* namely, Paratype P4918 Tantabiddy Well (C-26), Yardie Creek Station, collected A.M. Douglas and G.F. Mees, 17/5/1960; P5813; Tantabiddy Well (C-26), Yardie Creek Station, collected A.M. Douglas, 22/7/1963; P7716; North West Cape area, collected R. Gredling, 1963-4.

The stomach contents of a large series of *Milyeringa veritas* in the collection of the American Museum of Natural History were extracted by MNF and examined in Perth. Material came from: AMNH 45497 (N=30) which included specimens collected by Nelson, Butler and Rosen from the west side of the Cape Range peninsula between Yardie Station and Yardie Creek on the afternoon of 2 April 1969; AMNH 48568 (N=20) which included specimens collected by Nelson, Butler and Rosen from the east side of Cape Range peninsula from Neds Well to Mowbowra Creek on the morning of 5 April 1969.

RESULTS AND DISCUSSION

Ophisternon candidum

Members of the stygofauna were found in the midgut of P5813, namely thermosbaenaceans (*Halosbaena tulki* Poore and Humphreys, 1992) and atyid shrimps (*Stygiocaris* sp.); sand grains to 1.2 mm diameter were also recovered. The hindgut of the same individual yielded only terrestrial taxa or taxa terrestrial as adults namely, slaters (Isopoda: Philosciidae) and dragonfly (Odonata) and dipteran larvae (Table 1). No gut contents were found in P4918 or P7716.

The gut contents and the habitat characteristics of the taxa would suggest that two feeding episodes had occurred in the first (hindgut) of which the eel foraged in an open cave habitat on a non-cave aquatic fauna (Odonata and Diptera larvae) as well as cryptic species accidentally in the water (philosciid isopod). During the subsequent feeding episode the eel foraged solely on the specialised subterranean aquatic (stygo-) fauna comprising sediment foraging species (*Halosbaena* and *Stygiocaris*).

No shrimps were taken from Tantabiddy Well (C-26) in the original collections (Mees 1962) or subsequently (Humphreys and Adams 1991; W.F. Humphreys, unpublished) although both *S. lancifera* and *S. styliifera* occur in an adjacent well (C-25, Kudamurra Well; Mees 1962; W.F. Humphreys and M. Adams, unpublished 1991). *Halosbaena* has not been collected from C-26 (Poore and Humphreys 1992; W.F. Humphreys, unpublished). Hence, these gut contents constitute the only records of *Stygiocaris* and *Halosbaena* from C-26.

The distribution of the genus *Ophisternon* has been described as Gondwanan (Rosen and Greenwood 1976) but a recent interpretation considered both the genus *Ophisternon* and the family Synbranchidae to have a Tethyan distribution (Banareescu 1990: 203). The latter interpretation would accord with the stygofauna of

Table 1 The gut contents of *Ophisternon candidum* in the collections of the Western Australian Museum.

Location	Identification	Reg. No.
Midgut	Thermosbaenacea, <i>Halosbaena tulki</i>	BES: 820
Midgut	Atyidae: <i>Stygiocaris</i> sp.	BES: 821
Midgut	Atyidae: <i>Stygiocaris</i> sp.	BES: 822
Midgut	Thermosbaenacea, <i>Halosbaena tulki</i>	BES: 823
Midgut	Thermosbaenacea, <i>Halosbaena tulki</i>	BES: 824
Midgut	Thermosbaenacea, <i>Halosbaena tulki</i>	BES: 825
Midgut	Sand to 1.2 mm diameter and residue	BES: 826
Hindgut	Isopoda: Philosciidae	BES: 817
Hindgut	Odonata, larva	BES: 818
Hindgut	Unidentified	BES: 819
Hindgut	Diptera, larva	BES: 856

Table 2 The gut contents of *Milyeringa veritas* from the American Museum of Natural History collections. ‘Fish N’ and ‘Prey N’ denotes the number of fish containing that prey item.

Side of peninsula AMNH number (N) Contents	West		East	
	45497 (N=23)		48568 (N=16)	
	Prey N(%)	Fish N(%)	Prey N(%)	Fish N(%)
No contents	–	8 (31)	–	4 (21)
Cockroaches	1 (5)	1 (4)	9 (53)	7 (37)
Isopods (Armadillidae)	14 (64)	12 (46)	2 (12)	2 (11)
<i>Stygiocaris</i> (shrimps)	1 (5)	1 (4)	1 (6)	1 (5)
Crustacea (probably <i>Stygiocaris</i>)	1 (5)	1 (4)	1 (6)	1 (5)
Trichopteran larvae	1 (5)	1 (4)	2 (12)	2 (11)
Ants	4 (18)	1 (4)	0 (0)	0 (0)
Unidentified insect parts	–	1 (4)	0 (0)	0 (0)
Worms?	0 (0)	0 (0)	1 (6)	2 (11)
Total	22	26	16	19

the Cape Range peninsula and that of the prey items (Humphreys 1993a, 1993d; Knott 1993). Indeed, an undescribed species of syncarid crustacean of the genus *Atopobathynella* (H.K. Schminke, pers. comm.) (Parabathynellidae, Bathynellacea) is the only element in the stygofauna of the Cape Range peninsula (and Barrow Island) that is clearly Gondwanan (W.F. Humphreys, unpublished).

Milyeringa veritas

Milyeringa individuals included specialised members of the stygofauna (*Stygiocaris* sp.) in its diet, the aquatic larvae of terrestrial species (caddis larvae), and terrestrial species accidentally in the water (isopods, ants and cockroaches) (Table 2). The identifiable contents were predominantly (79%) terrestrial species that had presumably fallen into the water and, at the most, only 10% were specialised members of the stygofauna.

Milyeringa on the west coast ate predominantly terrestrial isopods (*Buddelundia* sp.), while those on the east coast fed mainly on cockroaches (Table 3); this distribution of prey items differs between coasts ($G = 16.868$, $P < 0.001$). Despite these differences the source of the food was predominantly from outside the water body, of terrestrial origin (Table 3).

Gudgeons examined for prey were larger ($F_s 1.43$

$= 28.75$, $P < 0.001$) on the west coast (38.5 ± 3.99 mm, $n = 26$) than on the east coast (30.6 ± 5.47 mm, $n = 19$), as were those ($F_s 1.31 = 17.5$, $P < 0.001$) in which prey was found (38.6 ± 4.39 mm and 31.2 ± 5.69 mm respectively).

Prey size was converted to common units (body length, mm) using empirically derived relationships – isopod length (mm) = 2.8 carapace width (mm) – 0.04 ($r^2 = 0.89$, $P = 0.017$); cockroach length (mm) = 3.9 head capsule width (mm) + 1.5. The mean head capsule width of the cockroaches was 1.3 ± 0.16 mm ($n = 8$) giving an estimated overall body length of 5 mm (by regression). The mean carapace width of the isopods was 2.9 ± 1.71 mm ($n = 6$) giving an estimated overall length = 8.1 mm (by regression). Hence, the bigger west coast fish were associated with bigger food items (isopods). However, as terrestrial Crustacea generally have an energy density only about 70% that of terrestrial insects (from Cummins and Wuycheck 1971), then the apparent advantage in food size may not confer an energetic advantage.

Associated fauna in the field

The fish share their habitat with a large number of stygofaunal elements, many of which were not represented in their gut contents (Table 4). The smallest taxa, such as copepods and ostracods, are probably outside the size range of prey items, which for *M. veritas* is known to include the length range of c. 2.8–14 mm, and for *O. candidum* 3 mm (*Halosbaena*) to an estimated 8 mm (Odonata). No fish samples were collected from known remiped habitat, although they do occur sympatrically (W.F. Humphreys, unpublished 1994). The melitid amphipods are sympatric with *M. veritas* (at locations C–24, 25, 105, 274 and 362; W.F. Humphreys, unpublished) and abundant in the stygal habitat but, despite being within the known size range of prey for both species of fish, they are not represented in the gut contents.

Table 3 Percentage contribution of prey, by taxa and origin, in the guts of *Milyeringa veritas* on the east and west coasts of the Cape Range peninsula ($n = 34$).

Group	West	East
Insects	12	29
Crustacea	47	12
Aquatic	12	9
Terrestrial	47	32

Table 4 Stygofauna associated with the two sympatric cave fishes on the Cape Range peninsula. $\sqrt{}$ = is known from the same sites but not recorded in the guts; + = is known from the same sites and not recorded in the guts; – = is not recorded from the same sites.

	<i>O. candidum</i>	<i>M. veritas</i>
<i>Stygiocaris lancifera</i> Holthuis	+ ¹	+
<i>S. styliifera</i> Holthuis	+ ¹	$\sqrt{}$
<i>Halosbaena tulki</i> Poore and Humphreys	+	$\sqrt{}$
<i>Haptolana pholeta</i> Bruce and Humphreys	–	$\sqrt{}$
Remipedia	–	$\sqrt{}$
Melitid amphipod gen. et sp. nov.	$\sqrt{}$	$\sqrt{}$
Calanoid copepods	$\sqrt{}$	$\sqrt{}$
Harpacticoid copepods	$\sqrt{}$	$\sqrt{}$
Ostracoda	$\sqrt{}$	$\sqrt{}$

¹ The species of *Stygiocaris* in *O. candidum* from C–26 is not known; immediately to the north of C–26 *S. styliifera* and *S. lancifera* are sympatric, while to the south only *S. lancifera* is known.

DISCUSSION

The prey identified is consistent with the behaviour of the fish. *O. candidum* inhabits the surface of, and burrows into, the faecal ooze characteristic of crustacean-rich stygal habitats. All the prey items identified are bottom dwellers or, in the case of the isopod, would sink to the bottom when it fell into the water. In contrast *M. veritas* moves widely through the water column, often hovering in mid- to surface waters where prey with hygrophobic integuments, such as cockroaches, would be encountered when they fell into the water.

The locations sampled for *M. veritas* include flooded sinkholes, small rock pools, shallow open caves in the coastal limestones, old wells (hand-excavated and lined with wood or cement) deep anchialine caves (i.e. inland caves connected at depth to the sea) and deep bores. From these samples the food of *M. veritas* comprised predominantly terrestrial taxa (79%) that have presumably fallen into the water; both the isopods and cockroaches are plentiful in some of the sampling locations as these cryptic taxa shelter there from the hot arid climate. However, there are populations of gudgeon known from caves (e.g. C–215, C–452) where such accidental food is unlikely to occur as the water is reached only at some horizontal distance from the entrance, or from 50 m deep bores. However, both these habitats contain rich stygofauna.

Both species of troglobitic fish are clearly opportunistic in their feeding, able to take accidental inputs of energy. The eel forages on the specialised subterranean inhabitants and the gudgeons must have this ability, although rarely recorded in these samples, because it inhabits some locations, such as C–215 and deep bores, essentially closed to accidentals. The gudgeons are capable of taking large and energy rich prey such as cockroaches, while the eels include prey of minute

size (*Halosbaena tulki* is <2 mm in total length; Poore and Humphreys 1992).

There is one area of bias in the data that impinges on the interpretation of these findings. From necessity the fishes were sampled at the few places where the stygal realm opens to the surface – wells and rockholes – and hence where epigean prey species would be present. Throughout the greatest part (>99.99%) of the distribution of this stygal community there are no known openings to the surface. Extensive sampling down boreholes has shown that the stygofauna is present in such areas, with the exception of *O. candidum* which was not sampled there, and that there was a general absence of epigean species in these areas (W.F. Humphreys, unpublished data, 1994). Hence, in general, the fish will be dependent on the stygofauna for food and not, as suggested by the data presented here, on epigean species accidentally in the water.

The stygal community on the Cape Range peninsula is unusual in that there are recorded only eight instances world wide of two species of sympatric cave fish (Thinès and Proudlov 1986), and because of their occurrence with a rich community of crustacea, many belonging to relict groups (Wägele 1992) such as thermosbaenaceans and remipedes (Poore and Humphreys 1992; W.F. Humphreys, unpublished). Given their Tethyan origins (Humphreys 1993a, 1993d; Knott 1993) it is not remarkable that the fish and crustaceans should be part of the same food web and the broad conservation implications are clear – the stygofauna is a functional community, changes to part of which may effect the remainder.

ACKNOWLEDGEMENTS

We thank Julianne Waldoock for her continued support, Dr G. Allen (WAM) for permission to dissect fish from the collections of the Western

Australian Museum and Dr H.K. Schminke for determining the syncarid.

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Manuscript received 7 December 1993; accepted 6 May 1994.

A new groenlandaspidid arthrodire (Pisces; Placodermi) from the Middle Devonian Aztec Siltstone, southern Victoria Land, Antarctica

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Abstract — *Boomeraspis goujeti* gen. et sp. nov is described from isolated trunk-shield plates found in the basal 30 metres of Aztec Siltstone exposed at Alligator Peak in the Boomerang Range of southern Victoria Land. *Boomeraspis* is characterised by its broad posterior dorsolateral plate (PDL) which has an inflected main lateral line canal and a strongly convex dorsal margin, and the posterior lateral plate (PL) features a strong lateral ridge. These features place *Boomeraspis* as a primitive member of the family Groenlandaspidae, distinguished from both *Tiaraspis* and *Groenlandaspis* by its proportionately longer PDL, strongly ridged and larger PL, and also by the long posterior division of the ventral lamina on the PVL plate.

INTRODUCTION

Devonian fossil fish remains were first collected from southern Victoria Land, Antarctica, in the summer of 1911–12 by Mr Frank Debenham, a member of Scott's "Terra Nova" expedition. His finds near Granite Harbour came from moraine material, and were later described by Woodward (1921), who correctly assigned a Devonian age to the small assemblage of fish scales, teeth and fragmentary bones. The first extensive collections were made *in situ* by B. M. Gunn and G. Warren during the 1955–1958 Transantarctic Expedition. More extensive collections of fossil fish were made in the summer of 1968–69 by members of the Victoria University of Wellington Antarctic Expeditions (VUWAE 13). Dr Alex Ritchie, of the Australian Museum, and Dr Gavin Young, Australian Geological Survey Organisation, made extensive collections of the Aztec Siltstone fishes over the summer of 1970–71 as part of VUWAE 15. White (1968) had described the fish remains collected by Gunn and Warren, and Ritchie (1972) summarised the distribution of the Aztec Siltstone fish faunas found on VUWAE 13, and later described the arthrodire *Groenlandaspis antarcticus* from the 1970–71 collection (Ritchie 1975). Young (1982, 1988, 1989a) has since described sharks, bothriolepid antiarchs and culmacanthid acanthodians, Young *et al.* (1992) have monographed the crossopterygian fauna, and Turner and Young (1992) have described the thelodonts. The Aztec Siltstone is now known to contain over 30 species of fossil fishes, making it one of the most diverse freshwater fish faunas of its age, and a keystone to biostratigraphic correlations within the East Gondwana Province (Young 1989b, 1993).

During the 1988/89 season Woolfe *et al.* (1990) discovered fish-bearing Aztec Siltstone in the Cook Mountains, nearly 100 km south of the previously

known sites. In the 1991/92 season the author joined M. Bradshaw, F. Harmsen and B. Staite in an expedition to collect fossil fish material from the Cook Mountains, and revisit known sites in the Skelton N  v   region. It will be several years before the vast amount of new material collected from that expedition is prepared and ready for description. This paper describes a new groenlandaspidid arthrodire based on a few isolated plates recovered from the southeastern spur of the Alligator Ridge region of the Boomerang Range (site 21, of Young 1988, Fig. 1). Other undescribed phlyctaeniid arthrodires are known from the Aztec Siltstone (e.g. Young 1991) although the material described here can be readily distinguished from these forms by showing features characteristic of the family Groenlandaspidae. Although two scant fish faunas have been reported from the higher units in section 21, the material described herein came from a lower fish-bearing horizon within the basal 30 metres of the Aztec Siltstone which may be identical with the fossiliferous horizon mentioned by Barrett and Webb (1973, section 3, as approximately 32 metres above the base of the unit) but not collected by them or by subsequent expeditions. All specimens are deposited in the collections of the Western Australian Museum (WAM).

Abbreviations used in the text and figures are: ADL, anterior dorsolateral plate; AL, anterior lateral plate; AVL, anterior ventrolateral plate; llc, main lateral-line canal groove; MD, median dorsal plate; ov.ADL, surface overlapped by ADL plate; ov.AL, area overlapped by AL plate; ov.MD, area overlapped by MD plate; ov.PL, area overlapped by PL plate; ov.PVL, area overlapped by PVL plate; PDL, posterior dorsolateral plate; PL, posterior lateral plate; PVL, posterior ventrolateral plate; ri,

ridges; Sp, spinal plate; tr.r, transverse ridge on lateral lamina of trunk-shield;

SYSTEMATICS

Order Arthrodira Woodward, 1891

Suborder Phlyctaenioidei Miles, 1973

Infraorder Phlyctaenii Miles, 1973

Family Groenlandaspididae Obruchev, 1964

Boomeraspis gen. nov.

Type species

Boomeraspis goujeti sp. nov.

Diagnosis

A groenlandaspidid arthrodire having a PDL which has an externally ornamented surface approximately as long as high, with a prominent vertical ridge developed ventral to the point of

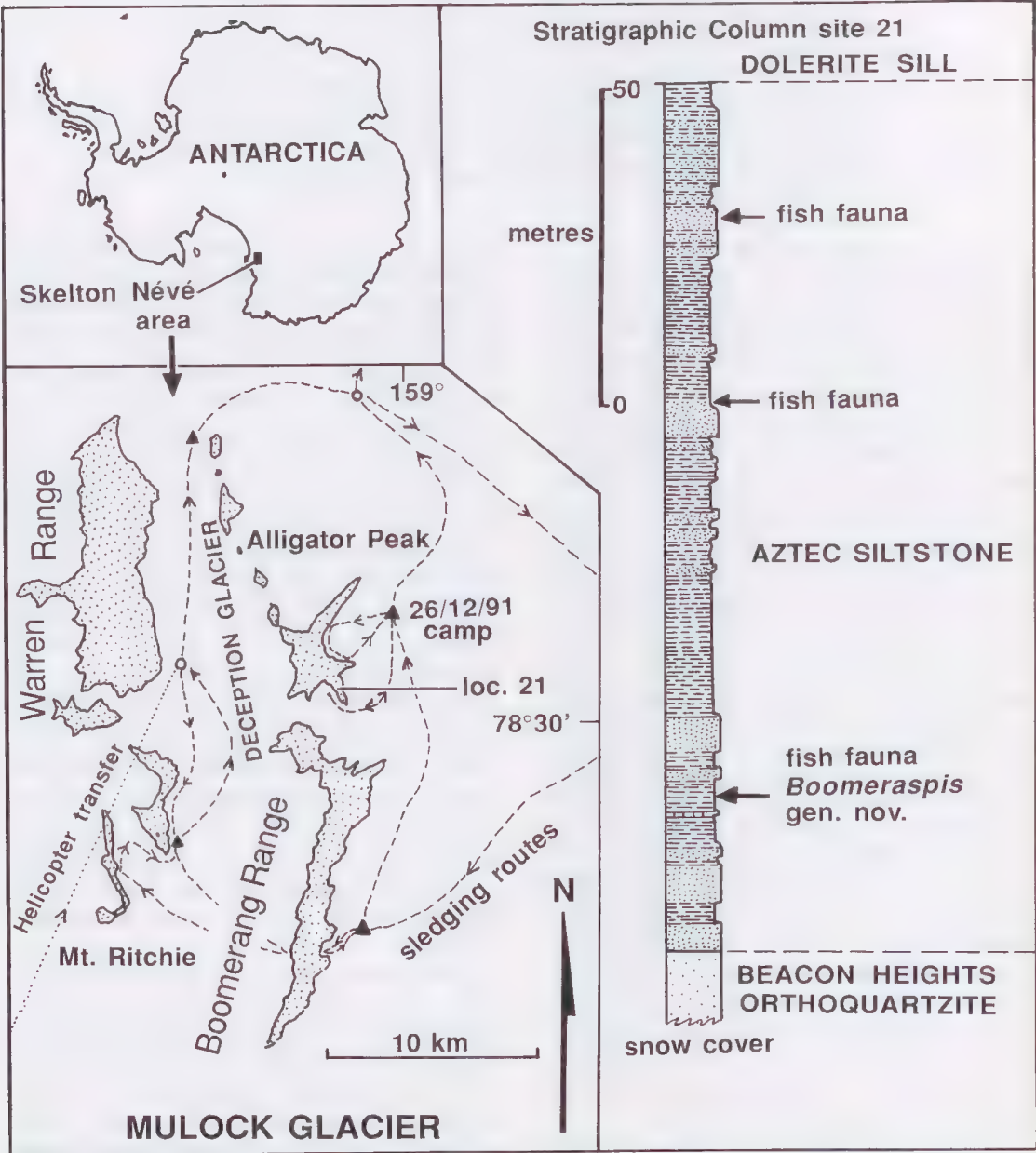


Figure 1 Locality map and stratigraphic section (after Young 1988) showing where the type collection of *Boomeraspis* material was found.

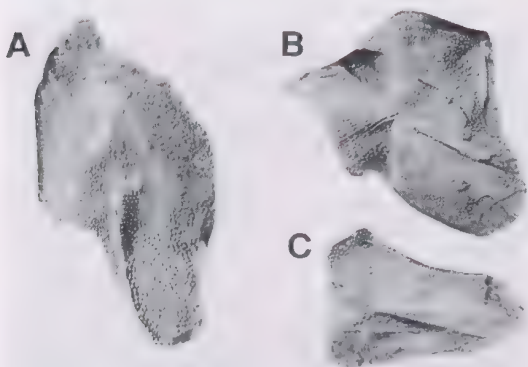


Figure 2 *Boomeraspis goujeti* gen. et sp. nov. A, paratype right PVL plate, WAM 93.7.4.; B, holotype right PDL plate, WAM 93.7.2; C, paratype right PL plate, WAM 93.7.3; All are latex peels whitened with ammonium chloride, $\times 1.5$.

inflection on the main lateral-line canal groove; PL has a prominent transverse ridge which becomes deeper anteriorly. Ornament on the PDL is of vertically directed rows of fine tubercles near the dorsal margin.

Remarks

Although known from only fragmentary material *Boomeraspis* is referred to the Groenlandaspidae because of the highly convex dorsal margin and inflected main lateral line canal on the PDL plate. It differs from the only other two known members of the family by its proportionately larger, strongly ridged PL plate, and the fact that the PDL is more elongated rostrocaudally compared with the narrow, higher PDLs seen in *Groenlandaspis* and *Tiaraspis*. The trunk plates described here are not considered likely to belong to *Antarctaspis* White 1968 because this genus has been referred to as a stem-group phyllolepid (Long 1984; Young 1991) and, based on these cranial similarities, the corresponding trunk-shield would be expected to be quite unlike that of groenlandaspidid arthrodires. Nor is *Boomeraspis* likely to be confused with *Antarctolepis* White, 1968 because the single plate of that genus, an AL, lacks a prominent lateral ridge that would be present on the AL of *Boomeraspis* as it has a prominent lateral ridge running anteriorly off the PL plate. Ritchie (1975) notes that *Antarctolepis* appears quite distinct in its AL plate from that of *Groenlandaspis*, and is therefore not likely to be confused with other members of that family.

Etymology

The generic name is after the locality (Boomerange Range) and the Greek "aspis" meaning "shield".

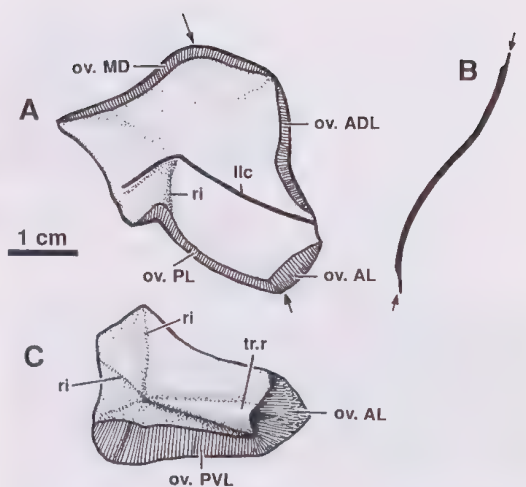


Figure 3 *Boomeraspis goujeti* gen. et sp. nov. A, B, right PDL plate, WAM 93.7.2 (holotype). A, lateral view; B, cross-sectional shape of external surface as indicated on A (internal surface unknown). B, right PL plate in lateral view (paratype WAM 93.7.3).

Boomeraspis goujeti sp. nov.

Figures 2–5, 6B

Diagnosis

Same as for genus.

Type material

Holotype WAM 93.7.2, an impression of the external surface of a complete right PDL plate (Figures 2B; 3A, B). Paratypes WAM 93.7.3, a complete right PL plate (part and counterpart; Figures 2C, 3C); WAM 93.7.4, a complete right PVL plate (part and counterpart; Figure 2A); WAM 93.7.5, an incomplete posterior division of a spinal plate (mostly impression only; Figure 4).

Etymology

The species name is for Dr Daniel Goujet of the Musée d'Histoire naturelle in Paris, for his contributions to arthrodire studies.

Locality and age

The specimens all come from a dark green laminated mudstone occurring immediately above the first thick bluff-forming sandstone unit, approximately 30 metres from the base of the Aztec Siltstone exposed along the southeastern spur of Alligator Ridge (locality 21 of Young 1988). All the specimens were found close together in loose slabs of mudstone scree on top of the outcrop. As all the plates are from the right side, and are of correct size to fit together, it is quite possible that they are

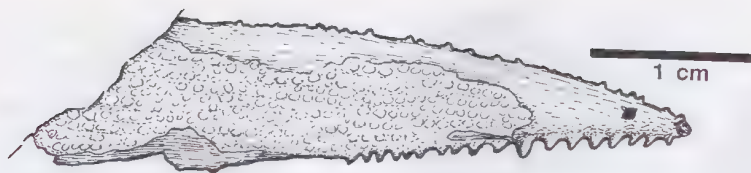


Figure 4 *Boomeraspis goujeti* gen. et sp. nov. Sp plate, as preserved. Camera lucida sketch; where the bone is missing the impression of the tubercular ornament in the rock is indicated, paratype WAM 93.7.5.

from the same individual. The unit from which the fish plates were collected also contains isolated thelodont scales of *Turinia antarctica*, and plates of an as yet undetermined species of *Bothriolepis*. *Boomeraspis* therefore comes from within either the *askinae* or *kohni* biozones of Young (1988), and could be regarded as late Givetian in age.

Description

The four isolated plates of *Boomeraspis* (Figures 2–4) may be used to give a tentative restoration of the overall shape of the trunk-shield (Figure 5), which assumes it was short and relatively high as in other groenlandaspids. The trunk-shield had a prominent lateral ridge running from the PL plate which presumably continued on to the AL plate, as for other phlyctaeniids, such as *Tiaraspis* (Gross 1962, Schultze 1984) and *Phlyctaenius* (Young 1983).

Posterior dorsolateral plate

The PDL (Figures 2A; 3A, B) measures 30 mm in rostrocaudal length along the dorsal margin, and is 42 mm in maximum depth as measured from the top of the dorsal margin to the anteroventral overlap area dividing the PL and AVL plates. The dorsal margin of the PDL tapers vertically (Figure 3B) suggesting that the two PDLs most likely met in contact underneath the MD plate as occurs in *Groenlandaspis*. The main lateral-line canal groove (llc, Figure 3A) is inflected through an angle of 120° in the posterior third of the plate, and there is a prominent vertical ridge (ri, Figure 3A) running from the point of inflection to the ventral margin of the plate. The posterior division of the main lateral-line canal is less well defined and does not extend all the way to the posterior margin of the plate. The ADL overlaps the PDL (ov.ADL, Figure 3A) for about two thirds the anterior margin, but does not overlap that section of the PDL containing the anterior end of the main lateral line canal groove. The overlap margins for the MD, ADL and PL plates (ov.MD, ov.ADL, ov.PL; Figure 3A) are slightly narrower than that for the AVL plate (ov.AL, Figure 3A). The inner surface of the PDL is not known.

Posterior lateral plate

The PL is a relatively large and distinctive plate

in *Boomeraspis* compared to that in other groenlandaspids (Figure 6), extending for nearly the length of the PDL plate. It has a subrectangular outline with a strongly convex dorsal margin (Figures 2C, 3C), and a gently curved posterior margin that is oriented almost vertically. The prominent lateral ridge (tr.r, Figure 3C) originates in the posterior third of the plate and increases in thickness evenly towards the anterior margin, appearing as a thick ridge on the lateral lamina. The ventral external margin of the PL (where the dermal ornament terminates) is almost straight, and the overlap areas for the PVL and AL (ov.PVL, ov.AL, Figure 3C) are both quite extensive, much broader than the overlap margins on the PDL plate. Unlike *Groenlandaspis* the PL of *Boomeraspis* lacks a posteroventral extension of the overlap area for the PVL plate. The ornament is of regularly spaced tubercles which are largest in the posterodorsal corner of the plate.

Posterior ventrolateral plate

The PVL (Figure 2A) is known from part and counterpart, although the anterior margins are not well preserved. It is a narrow plate having a lateral lamina extending just over half the plate length. The posterior margin of the lateral lamina is evenly

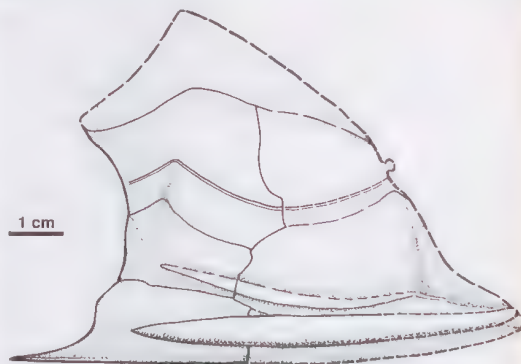


Figure 5 *Boomeraspis goujeti* gen. et sp. nov. Attempted restoration of the trunk shield based on the presence of the PVL, PL, PDL and Sp plates and their margins with neighbouring plates. Extent of the anterior trunk-shield plates and shape of the MD plate is based on comparisons with other groenlandaspids.

curved, meeting the ventral lamina along a prominent ventrolateral ridge. This ridge is only present in the posterior half of the plate. A less prominent, but still well-defined ridge is developed from the anterodorsal corner of the lateral lamina running posteroventrally towards the ventrolateral ridge, but tapering out well before reaching it. A small section of the overlap area for the AL plate is preserved, indicating that an extensive overlap was developed between the two plates. The ornament of the PVL consists of very fine, small tubercles for most of the plate, with larger, coarse tubercles present on the posterior half of the ventral lamina. The PVL differs from that of *Groenlandaspis* and *Tiaraspis* in its narrower ventral lamina and presence of a weak ridge running posteroventrally from the anterior corner of the lateral lamina.

Spinal plate

The Sp plate is almost completely preserved, missing only a section of the anterior region. It shows small pointed tubercles along the lateral margins and a row of slightly larger, recurved

tubercles lining part of the the mesial edge that protected the lateral edge of the pectoral fin. The bone is absent from most of the surface of the Sp, but impressions of the ornament show rows of aligned tubercles covered the external surface. In general form it is quite similar to the Sp in *Groenlandaspis* (Ritchie 1975).

PHYLOGENETIC POSITION OF BOOMERASPIS

Boomeraspis is placed within the family Groenlandaspidae because of its deep PDL plate which has a strongly inflected main lateral-line canal groove and a well-rounded, convex dorsal margin (Ritchie 1975, Goujet 1984). Although the inner surface of the PDL is unknown, the cross-sectional shape of the external surface is very similar to that of *Groenlandaspis* and suggests that it is likely that the two PDLs either met in dorsal contact or were closely situated under a high MD plate. Within the Groenlandaspidae only three genera are currently known, although others have been recognised and are currently being studied from the Early-Middle Devonian Mulga Downs Group of New South Wales by Dr Alex Ritchie (Ritchie 1975, p.571 "a new undescribed form from the Mulga Downs Group"). Clearly to resolve the question of whether *Boomeraspis* is more closely related to *Groenlandaspis* or to *Tiaraspis* depends largely on finding more complete remains, especially the head-shield.

The primitive condition in all phlyctaeniids, based on the Early Devonian species from Spitsbergen and Canada (Goujet 1984, Young 1983), is to have an elongate trunk-shield which has very long PL and PDL plates, and the PDL carries a straight lateral-line canal groove. The PL plate in most primitive phlyctaeniids may have a well-developed lateral ridge present (e.g., *Phlyctaenius*; Young 1983; arctolepids, arctaspids; Goujet 1984). Comparisons of the trunk-shield morphology would suggest that *Boomeraspis*, by having relatively longer PDL and PL plates, and a ridge on the lateral lamina of the PL plate, is more plesiomorphic than either *Tiaraspis* or *Groenlandaspis*. *Groenlandaspis* is considered more derived than *Tiaraspis* and *Boomeraspis* in having a PL plate that lacks any lateral ridge and has a well-developed, posteriorly-directed overlap surface for the PVL plate. The only synapomorphy that seems to unite *Boomeraspis* with either *Tiaraspis* or *Groenlandaspis* is the shape of the dorsal margin of the PDL plate, which in *Groenlandaspis*, and apparently (assumed in *Boomeraspis*) meets the opposing PDL underneath the MD plate. Both Ritchie (1975) and Schultze (1984) used this feature as an autapomorphy of the genus *Groenlandaspis*, so its suggested presence in *Boomeraspis*, based on

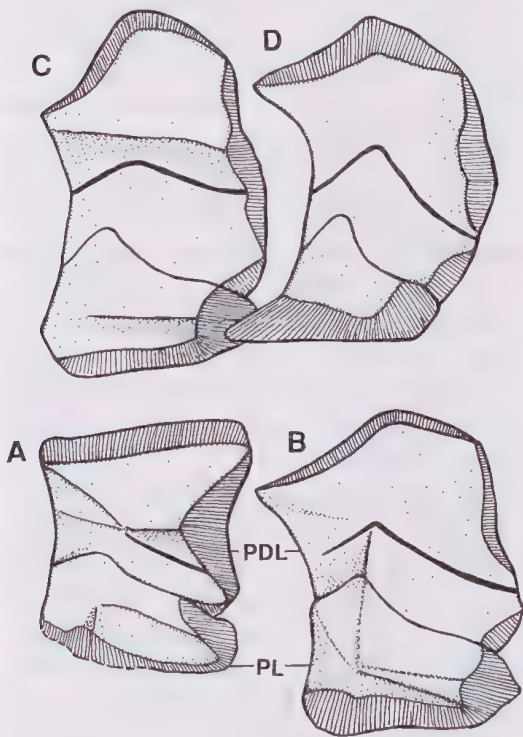


Figure 6 Comparison of right PDL and PL plates of A, *Phlyctaenius stenosis* (after Young 1983); B, *Boomeraspis goujeti* gen. et sp. nov.; C, *Tiaraspis subtilis* (modified after Gross 1962, and Schultze 1984), and D, *Groenlandaspis antarcticus* (after Ritchie 1975). Not to scale.

the external form of the PDL (Figure 3B), would support a sister-group relationship to *Groenlandaspis*.

The groenlandaspidid arthrodires range from the Early Devonian (Siegenian-Early Emsian) of Germany (*Tiaraspis subtilis*) to the very end of the Devonian (*Groenlandaspis*, Givetian-late Famennian, Antarctica, Australia, Middle East; Janvier and Ritchie 1977; Famennian of the East Greenland and Europe; Ritchie 1975), and possibly the Lower Carboniferous of Turkey (Janvier *et al.* 1984). The presence of several undescribed groenlandaspidids in the Early-Middle Devonian Mulga Downs Group of New South Wales and of several species of *Groenlandaspis* in the Givetian Aztec Siltstone (Dr A. Ritchie pers. comm. 1993) would suggest that the East Gondwana Province was a centre of radiation for the groenlandaspidids, immediately following the Gondwana origin for the group sometime in the Early Devonian (Germany may have then part of the northern margin of Gondwana; Young 1987a, 1987b). Although most groenlandaspidids occur in freshwater red-bed or alluvial sequences, the presence of one ADL plate of *Groenlandaspis* sp. (WAM 91.4.35) in the bedded marine limestones of the lower Frasnian Gneudna Formation, Carnarvon Basin, Western Australia, shows that the genus was capable of dispersal by marine routes.

ACKNOWLEDGEMENTS

Fieldwork in Antarctica over the 1991/92 season was funded through ASAC grant 136 to Long, and I thank the Trustees of the Western Australian Museum for their support of the Museum's involvement in the expedition. Sincere thanks to my colleagues in the field, Margaret Bradshaw, Fraka Harmsen and Brian Staite, for their assistance and support during the two months spent working in southern Victoria Land, and to Gavin Young (AGSO, Canberra) and Alex Ritchie (Australian Museum) for allowing me access to collections in their care and helpful discussion of the work. Gavin Young, Alex Ritchie and Philippe Janvier (Musée d'histoire naturelle, Paris) are thanked for critically reviewing the paper. Kris Brimmell is thanked for her fine photography of the specimens, and Kate Trinajstić for her help editing the manuscript.

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Manuscript received 9 August 1993; accepted 8 April 1994.

A new species of *Melomys* (Rodentia, Muridae) from Yamdena Island, Tanimbar group, Eastern Indonesia

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Abstract — Seven specimens of *Melomys*, superficially most similar morphologically to members of the *M. leucogaster* group (*sensu*, Tate 1951), were recently collected in Yamdena Island, eastern Indonesia. They are herein described as a new species.

INTRODUCTION

In April–May 1993, a team of vertebrate biologists from the Western Australian Museum and the Museum Zoologicum Bogoriense, collected seven specimens of *Melomys* from Yamdena Island, Tanimbar group, Maluku Tenggara. The combination of medium to large size (body and pes lengths greater than 120 mm and 25 mm, respectively), a short, broad skull, short rostrum, fur on ventral surface white to base and only one hair for each tail scale, identify these specimens as belonging to the *Melomys leucogaster* – *M. rufescens* group (Rümmmler 1938, Tate 1951). These Tanimbar specimens are herein described as a new species.

METHODS

The Tanimbar specimens were weighed in the field prior to their fixation with formalin. External measurements were recorded from these specimens following their fixation, except for the skin and skull WAM M43821, which was measured prior to fixation. All measurements (in mm) were taken with digital callipers: externals to 0.1 mm; skull and dental to 0.01 mm. Measurement points follow Tate (1951). Pelage and colour descriptions, where they were determined from the colour charts of Smithe (1975), are capitalised.

Adult condition was judged by reproductive status only, because basicranial sutures were still clearly visible in specimens of Tanimbar *Melomys* that were reproductively mature and had very worn teeth.

THE *MELOMYS LEUCOGASTER* – *M. RUFESCENS* "GROUP"

Rümmmler (1938) placed the following forms as subspecies of *M. leucogaster*: *M. l. leucogaster* (Jentink, 1908) (including *M. latipes* Tate and Archbold, 1935); *M. l. arcium* (Thomas, 1913); *M. l. fulgens* (Thomas, 1920); *M. l. talaudium* (Thomas, 1921) and *M. l. caurinus* (Thomas, 1921).

Tate (1951) considered *M. arcium*, *M. fulgens*, *M. caurinus* and *M. talaudium* to be species. He retained *M. latipes* and *M. rubicola* Thomas, 1924 as subspecies of *M. leucogaster* but stated that "I am almost of the opinion that they should be reduced to synonyms of *M. leucogaster*". Laurie and Hill (1954) considered that *M. leucogaster* comprised only *leucogaster* and *latipes*. They considered *rubicola* a species and listed *talaudium* and *caurinus* as subspecies of *M. fulgens*.

Rümmmler (1938) considered that *M. rufescens* comprised three subspecies: *M. r. rufescens* (Alston, 1877); *M. r. gracilis* (Thomas, 1906) and *M. dollmani* Rümmmler, 1935. Tate (1951) added the following subspecies: *M. r. bougainville* Troughton, 1936; *M. r. stalker* (Thomas, 1904); *M. r. sexplicatus* (Jentink, 1907); *M. r. hageni* Troughton, 1937; *M. r. niviventer* Tate, 1951 and *M. r. calidior* (Thomas, 1911). He placed *Mus musavora* Ramsay, 1877 in synonymy with *M. r. rufescens*. Laurie and Hill (1954) largely followed Tate (1951) but placed *dollmani* in synonymy with *gracilis*.

TAXONOMY

Melomys cooperae Kitchener sp. nov.

Figures 1–3, Table 1

Holotype

Museum Zoologicum Bogoriense specimen number 15902; adult (pregnant) female; weight 65 g; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; liver preserved at the Western Australian Museum in ultrafreeze refrigerator. Collected in breakback trap on 2 May 1993 by R.A. How and D.J. Kitchener.

Type locality

1 km S Kebun Lorulun, c. 20 km N Saumlaki, Yamdena Island, Tanimbar group; Maluku Tenggara, Indonesia (7°52'S, 131°25'E); altitude 200 m.

Paratypes

All collected at Lorulun; all alcoholic specimens, except Western Australian Museum No. (WAM) M43821, which is a skull and cabinet skin; all adult, except WAM M43823 which is a subadult.

WAM (M43621–22, M43821), 4 ♀ ♀; WAM (M43746, M43820, M43823) 3 ♂ ♂.

Diagnosis

Melomys cooperae is diagnosed from all other species of *Melomys* by its large last upper molar (M³) and combination of very long tail, long incisive foramen and distinctive white cheeks.

Description

Measurements of skull, dentition and externals are presented in Table 1.

Skull (Figure 1)

Skull of moderate size: greatest skull length 36.7 (36.0–38.0) and zygomatic width 18.2 (17.2–18.9), with a relatively narrow and short rostrum. Skull dorsal profile gently curved from nasal distal tip to parietal mid point when it curves more sharply downward to external occipital crest; interparietal wide 9.8 (9.1–10.5); parietal moderately inflated; frontal posterior part very slightly inflated but anteriorly forms a slight median sulcus that reaches

Table 1 Measurements (in mm) of the skull, dentition, and externals and weight (g) of *Melomys cooperae* sp. nov. holotype and paratypes and *M. leucogaster latipes*.

CHARACTER	M.l. latipes M.l.latipes								
Museum number	Holotype MZB15902	WAM 43621	WAM 43622	WAM* 43821	WAM 43746	WAM 43820	WAM 43823	* AM13781	* AM13815
Age/Sex	A ♀	A ♀	A ♀	A ♀	A ♂	A ♂	SA ♂	A ♀	A ♂
Greatest skull length	36.20	—	—	36.48	36.03	38.02	34.83	—	36.99
Condylolincisor length	32.95	33.86	—	33.97	32.84	35.04	31.29	—	36.83
Zygomatic width	18.31	18.49	17.17	18.72	17.91	18.86	17.23	—	21.17
Interorbital breadth	5.66	5.81	5.68	5.98	5.70	5.61	5.29	6.79	6.73
Interparietal breadth	10.51	9.11	—	9.63	9.99	9.85	10.01	—	10.43
Braincase breadth	14.87	14.78	15.27	15.02	14.97	14.74	14.86	15.21	15.55
Mastoid width	12.57	12.43	—	12.81	12.83	13.06	12.42	—	14.38
Nasal length	12.80	—	11.35	11.82	11.87	13.08	12.31	11.65	11.58
Nasal breadth	4.31	4.50	3.97	4.77	4.28	4.59	4.60	4.23	4.15
Zygomatic plate breadth	4.76	4.83	4.27	5.22	4.85	5.08	4.71	4.79	5.28
Diastema length	8.68	9.67	8.93	10.10	9.07	10.06	8.88	10.62	11.12
Height muzzle (behind ant. pal. for.)	9.53	9.41	8.72	9.27	9.01	9.34	8.67	9.73	9.74
Palatal length	17.28	18.02	17.24	18.36	17.64	18.81	16.92	19.04	19.60
Ant. palatal foramen length	4.70	5.98	5.53	5.74	5.58	6.18	5.12	5.29	5.44
Ant. palatal foramen breadth	2.29	2.26	2.17	2.28	2.46	2.29	2.26	2.44	2.76
Mesopterygoid fossa breadth	3.06	2.93	2.60	3.10	2.98	3.09	3.15	3.14	3.20
M ¹ –M ¹ breadth (inside)	2.99	3.24	2.84	3.42	3.03	3.34	2.89	3.46	3.91
Bulla length	5.06	5.34	—	5.52	5.05	5.17	4.97	4.92	4.69
M ¹ –M ³ crown length	6.87	6.82	6.46	6.31	6.73	6.58	6.52	6.86	6.72
M ¹ –M ³ alveoli length	7.08	7.10	6.61	6.64	7.00	6.99	6.68	7.04	6.95
M ¹ crown length	3.79	3.33	3.69	3.42	3.57	3.25	3.58	3.65	3.35
M ¹ crown breadth	2.00	2.02	1.84	2.01	2.02	1.84	2.12	2.13	2.01
M ² crown length	2.53	2.40	2.17	2.55	2.51	2.50	2.50	2.79	2.57
M ² crown breadth	1.94	2.02	2.01	1.99	2.03	1.80	2.04	2.10	1.99
M ³ crown length	1.39	1.64	1.61	1.50	1.52	1.60	1.53	1.57	1.78
M ³ crown breadth	1.44	1.42	1.44	1.46	1.38	1.37	1.41	1.52	1.43
Dentary length	21.42	20.73	19.16	20.59	20.17	21.46	19.60	22.64	23.91
M ₁ M ₁ (crown) length	7.02	6.69	6.46	6.54	6.49	6.46	6.53	7.28	6.84
Snout to vent length	128.0	135.7	118.1	137.0+	131.6	139.5	112.7	150.0*	160.0*
Tail to vent length	154.5	170.0	139.7	155.0+	142.0	158.4	140.5	151.0*	—
Ear length (from basal notch)	17.2	18.4	16.9	18.5+	16.3	19.7	16.6	17.0*	15.9*
Pes length (without claw)	27.0	25.8	24.8	25.3+	27.7	28.1	26.8	29.7*	31.0*
Pes breadth at base of digit V	8.2	7.7	7.4	5.6+	7.8	8.4	7.6	7.3	7.7
Tibia length	34.4	37.3	33.5	—	36.5	40.1	34.0	—	—
Weight (gm)	65.0	81.0	64.5	72.0	80.0	96.5	60.0	122*	146*
Scale No./cm	12	12	14	—	12.5	11.5	14	—	—

* Skin and skull
+ From recently killed animal

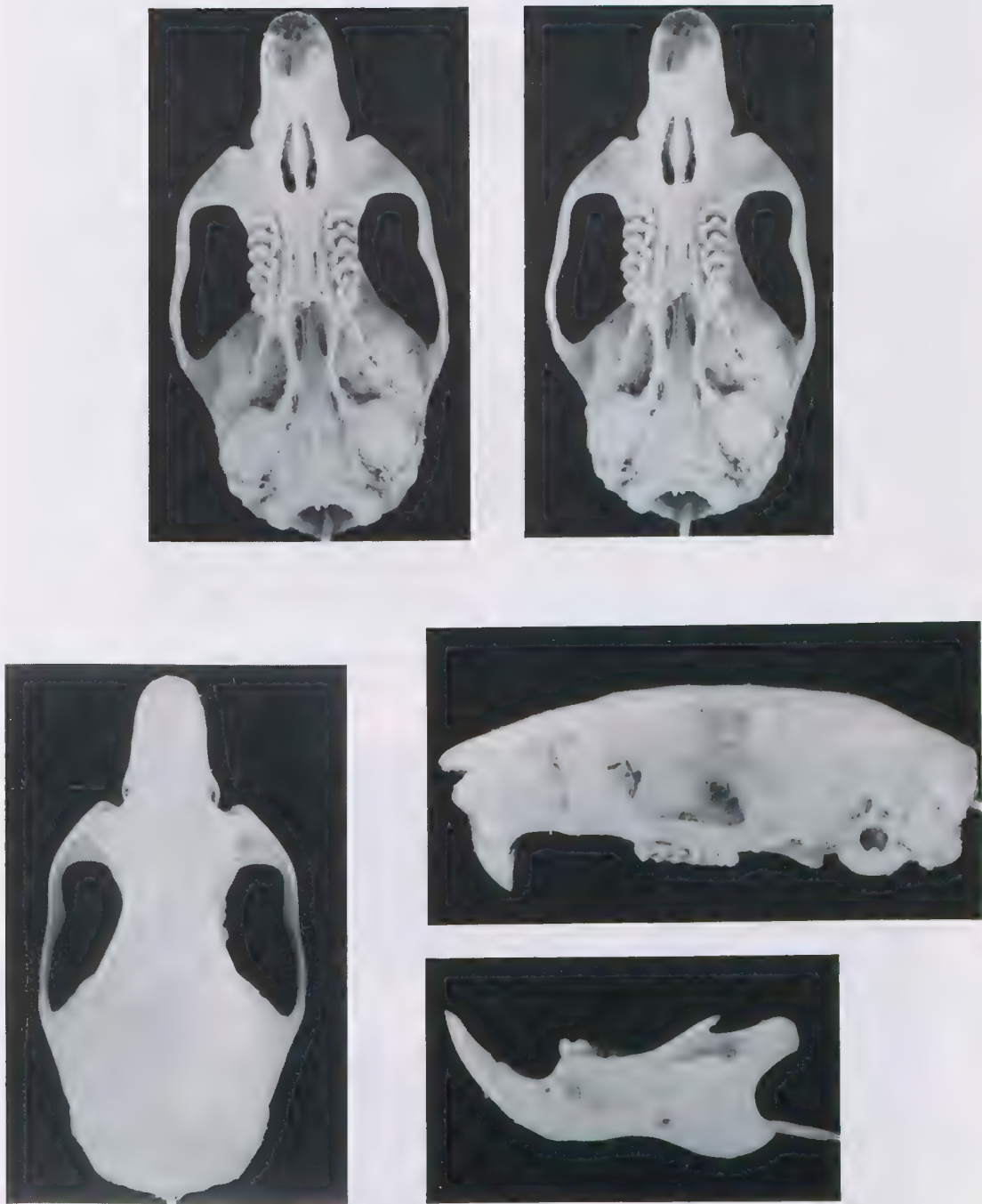


Figure 1 Plates of dorsal, ventral (as stereopairs) of the skull and lateral surface of the skull and dentary of holotype of *Melomys cooperae* sp. nov., holotype.



Figure 2 Plate of the tail and of the pes plantar surface of *Melomys cooperae* sp. nov., holotype.

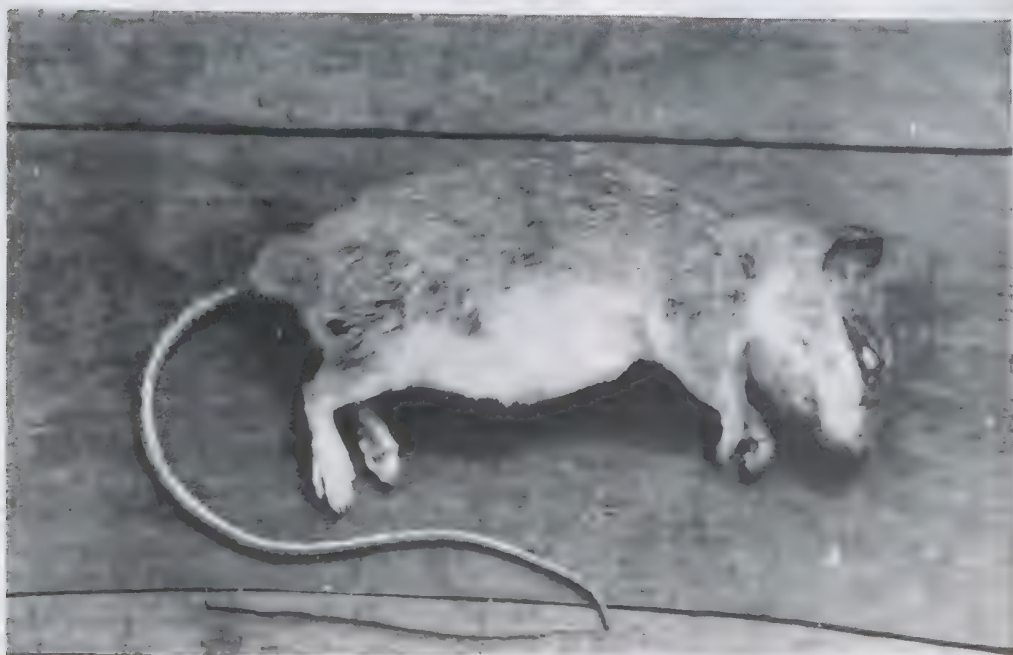


Figure 3 Photograph of *Melomys cooperae* sp. nov. taken shortly after its death. (Photograph by Dr R.A. How).

to posterior one-quarter of nasal; nasal short 12.2 (11.4–13.1), sharply constricted proximally and flared to a breadth of 4.4 (4.0–4.8) distally; anterior edge of premaxilla flange projected dorsally above incisor, almost vertical, or slightly convex leading edge – nasal projects to a point approximately above or slightly anterior to this leading edge; zygomatic arch moderately thickened with the ventral part of malar process broadest; zygomatic plate broad 4.8 (4.3–5.2), anterior leading edge almost vertical; infraorbital fissure moderately wide; lachrymal bones moderate, project only slightly outside the anterointernal curve of the orbit edge; post-squamosal hook moderately well developed (the holotype has a noticeable proximal dorsal projection), forms a slight vertical ridge with lateral occipital and mastoid, this ridge does not progress to interparietal posterior margin; postglenoid foramen small, semioval; temporal ridges slight, from frontal/parietal suture a fainter beading traverses dorsolateral margin of parietal to interparietal; rostrum narrow with posterolateral swelling only slightly inflated; anterior palatal foramen vary in length (4.7–6.2) but terminate posteriorly well anterior of M^1 anterior alveolus, broadly bowed but slightly wider posteriorly; palate narrow with upper tooth rows diverging posteriorly; mesopterygoid and parapterygoid fossae narrow; foramen oval ventral fossa small; bulla long 5.2 (5.1–5.5), moderately inflated, with long and robust eustachian process; internal pterygoid process diverge posteriorly, terminate anterior to eustachian process.

Dentition (Figure 1)

Molars large, M^3 larger than all other species of *Melomys* (cf Menzies 1991: Fig 3), particularly anterolingual cusp; M^1 anterior and intermediate lamellae with well developed lingual cusps; posterior lamella without lingual cusp but with lingual and buccal posterior extensions which enclose a distinct, centrally-placed fossa (on moderately worn teeth, this is evident as an isolated enamel ring entirely within the posterior lamella); M^2 with large anterolingual cusp only remaining of anterior lamella, intermediate and posterior lamellae well developed. The latter with posterior fossa as on M^1 . M^3 with anterolingual cusp well developed, separate from posterior lamella; molar rows diverge posteriorly from each other; upper incisors opisthodont, anterior face orange. First and second lower molars each with well-developed posterior cingulum; M_1 with small but distinct anterior moiety, soon merging with intermediate lamella as result of wear.

Externals (Figures 2 and 3)

Moderate body size with snout to vent length

132 (118–140) 6 and weight 76.5 (64.5–96.5) g. Tail long 153 (140–170) 6 and averaging 116% of body length; ears long 17.8 (16.3–19.7) 6; pes moderately long 26.5 (24.8–28.1) 6, narrower than *M. leucogaster latipes*. Scales on tail not raised to form a ridge or hump (Figure 2). Plantar pads of pes and manus typical of *M. l. leucogaster*, *M. l. latipes* and *M. rufescens* from Aru Islands. There are two pairs of inguinal teats.

Pelage

Dominant colour of dorsal surface pelage Cinnamon Brown resulting from Cinnamon Brown and/or Black tipping to the Medium Neutral Gray colour of basal three-quarters of hairs. Head contrastingly coloured. Black tipping more prominent on rostrum and forehead evenly grading into Cinnamon Brown of temporal region, but contrasting with White of cheeks – dark rings around eyes further highlights this contrast. Hairs in mid dorsum with length of 9 while those of mid forehead 7; flanks Cinnamon tipping to the Medium Neutral Gray of basal two-thirds of hairs. Lips, cheek to just beneath eye, throat, chest, abdomen to anus, inside of thigh, manus and pes upper surface White; interface between White of abdomen and Cinnamon of flanks Medium Neutral Gray as Cinnamon tipping of hairs becomes more sparse. Abdomen hairs 5–6 long; outer leg surface Cinnamon. Proximal two-thirds of ear pinna skin Cinnamon, distal one-third Dark Neutral Gray; pinna lightly furred inside and outside with short Cinnamon Brown hairs. Tail skin Gray Lavender dorsally and a paler Pale Neutral Gray ventrally.

Tail scales with one hair per scale; tail hairs moderately long, three-quarters scale breadth.

Habitat

Six of the specimens, including the holotype, were captured in breakback traps set on the ground in open (15–30% canopy cover), tall (to 30 m), disturbed vine forest (Figure 4) with the following genera of trees prominent: *Ficus*, *Erythrina*, *Podocarpus*, *Albizia* as well as 'Kenari' trees. The understorey was mostly *Lantana*. There were numerous vines and creepers (Figure 4). The western edge of the trapping site had a small stream with the freshwater mangrove *Barringtonia* (fidé R.E. Johnstone).

One specimen (M43746, adult male) was trapped in a breakback trap in a pure association of Alang Alang grass (*Imperata cylindrica*) that adjoined the above described vine forest.

Reproduction

The two adult females collected on 18 April 1993 were pregnant. Both had two fetuses in the right uterine horn and none in the left horn. The crown



Figure 4 Photograph of the habitat at Lorulun, Yamdena Island – type locality of *Melomys cooperae* sp. nov. (Photograph by Dr R.A. How).

to rump lengths of one set of these foetuses was c. 14.5 and the other c. 19.2. Of the two females collected two weeks later on 2 May 1993, one had two near-term foetuses (crown to rump lengths 30.2 and 39.3), with one in each uterine horn; the other female appeared to have recently given birth because its uterine horns were large, incompletely involuted and extremely vascular along their internal margin (although no clear implantation sites were apparent). The two males collected on 2 May had scrotal testes with prominent epididymides. The male collected on 18 April (WAM M43823) was subadult and had small abdominal testes with dimensions of 4.1 x 6.5.

Distribution

Known only from the type locality, Lorulun, Yamdena Island.

Remarks

Melomys cooperae may be confused superficially with some of the forms which have been associated with *M. leucogaster*. A number of these forms are known from the type or a few specimens only, which we were not able to examine. We have, then, depended on the original type descriptions and measurements of most of these forms in Rümmler (1938), Tate (1951), Menzies and Dennis (1979), but made direct comparison with two reference specimens of *M. l. latipes* from Papua New Guinea. The measurements presented below are of adult

specimens only (mean, range, sample size).

Melomys cooperae differs from *M. l. leucogaster* in having a generally smaller body e.g., snout to vent (body) length 132 (118–140) 5 v. (154–195) 4; tail generally longer relative to its snout to vent length 1.18 (1.08–1.25) 6 v. 0.95 (0.81–1.11) 5; pes length shorter 26.5 (24.8–28.1) 5 v. 31–36 (4). Skull smaller: e.g., zygomatic width smaller 18.2 (17.2–18.8) 6 v. 21.4 (21.2–21.5) 2; interorbital breadth smaller 5.7 (5.6–6.0) 6 v. 6.7 (6.7–6.7) 2; nasals shorter 12.2 (11.4–13.1) 6 v. 13.9 (13.8–14.0) 2; palate shorter 17.9 (17.2–18.8) 6 v. 21.1 (21.2–21.2) 2; palatal breadth inside M^1 narrower 3.1 (2.9–3.4) 6 v. 3.7 (3.5–3.8) 2; bulla longer relative to palatal length 0.291 (0.275–0.301) 5 v. 0.238 (0.231–0.245) 2; M^{1-3} crown length shorter 6.6 (6.5–6.9) 6 v. 7.5 (7.1–7.8) 2.

It differs from *M. leucogaster latipes* in having a longer tail relative to its snout to vent (body) length 1.16 (1.08–1.25) 5 v. 1.02 (1.01–1.03) 2; pes length shorter 26.5 (24.8–28.1) 5 v. 30.9 (29.7–32.0) 3; pes and manus paler, predominantly white rather than a darker brown dorsally; cheeks white to edge of eye which is encircled by dark coloured ring rather than as in *latipes* where cheek colour same as forehead and without dark circles around eyes. Skull with rostrum longer and narrower, without marked inflations of posterolateral rostral bulbs such as occurs in *latipes*; nasal terminates distally approximately level with antermost face of premaxillary dorsal wing, rather than well

posterior to that face; skull narrower: e.g., interorbital breadth 5.7 (5.6–6.0) 6 v. 6.6 (6.3–6.8) 3; zygomatic width 18.2 (17.2–18.9) 6 v. 20.6 (20.0–21.2) 2 and braincase breadth 14.9 (14.7–15.3) 6 v. 15.4 (15.2–15.6); bulla longer 5.2 (5.1–5.3) 5 v. 4.9 (4.7–5.0) 3, considerably more inflated; ventral opening of foramen oval much smaller than in *latipes*; much more deeply incised sulcus running anterior of the sphenorbital fissure.

It differs from *M. rubicola* in having White cheeks, neck and back dark brown rather than strongly ochraceous; pes shorter 26.5 (24.8–28.1) 5 v. 31; tail shorter 153 (142–170) 6 v. 180; skull approximately same length but zygomatic width smaller 18.2 (17.2–18.9) 6 v. 19.

It differs from *M. arcium* in having White cheeks; tail longer rather than shorter than body length; tail longer 153 (142–170) 6 v. 127; skull smaller, e.g., condyloincisor length shorter 33.7 (32.8–35.0) 6 v. 38.1; zygomatic width narrower 18.2 (17.2–18.8) 6 v. 20.7; interorbital breadth narrower 5.7 (5.6–6.0) 6 v. 6.9; nasal shorter 12.2 (11.4–13.1) 5 v. 13.7; bulla larger 5.2 (5.1–5.5) 6 v. 4.7, longer relative to condyloincisor length 0.156 (0.148–0.163) 5 v. 0.123; M^{1-3} crown length smaller 6.6 (6.3–6.9) 6 v. 7.1.

It differs from *M. fulgens* in having dorsum dark brown and cheeks White rather than a vivid light orange brown (ochraceous) dorsum and no White cheeks; ears without whitish patch behind base; body length shorter 132 (118–140) 6 v. 150; tail shorter 153 (142–170) 6 v. 200; tail shorter relative to body length 1.16 (1.08–1.25) 5 v. 1.33; pes much shorter 26.5 (24.8–28.1) 5 v. 34; zygomatic width narrower 18.2 (17.2–18.9) 6 v. 22.2; interorbital breadth narrower 5.7 (5.6–6.0) 6 v. 7.0; palatal breadth narrower inside M^1 3.1 (2.8–3.4) 6 v. 3.8; palatal length shorter 17.9 (17.2–18.8) 6 v. 19.5; bulla longer relative to palatal length 0.291 (0.275–0.301) 5 v. 0.262; and M^{1-3} crown length shorter 6.6 (6.3–6.9) 6 v. 7.1.

It differs from *M. talaudium* in having one hair per tail scale rather than three; dorsum a dark brown and cheeks White rather than a vivid ochraceous dorsum and cheeks not White; body and tail length shorter, approximately as for *M. fulgens*; pes shorter 26.5 (24.8–28.1) 5 v. 30.5; zygomatic width narrower 18.2 (17.2–18.9) 6 v. 20.9; palate narrower inside M^1 3.1 (2.8–3.4) 6 v. 3.9; bulla much longer relative palatal length 0.291 (0.275–0.301) 5 v. 0.186; M^{1-3} crown length much shorter 6.6 (6.3–6.9) 6 v. 7.6.

It differs from *M. caurinus* in having dorsum a dark brown and cheeks White rather than dorsum orange brown (Tate 1951) and cheeks not White [although Rümmler (1938) described the pelage colour of the type as affected by immersion in alcohol]; tail much longer relative to body length 1.16 (1.08–1.25) 5 v. 0.8; scales on tail flat and not raised as round humps as in *caurinus*; ear much

longer 17.8 (16.3–19.7) 6 v. 10; pes shorter 26.5 (24.8–28.1) 5 v. 29.5; skull narrower, e.g., zygomatic width 18.2 (17.2–18.8) 6 v. 20.0; interorbital breadth 5.7 (5.6–6.0) 6 v. 6.4; palatal breadth inside M^1 3.1 (2.8–3.4) 6 v. 3.5; skull shorter, e.g., diastema length 9.4 (8.7–10.1) 6 v. 10.6; palatal length 17.9 (17.2–18.8) 6 v. 20.3; bulla longer 5.2 (5.1–5.5) 6 v. 4.8, also longer relative to palatal length 0.291 (0.275–0.301) 5 v. 0.237; and M^{1-3} crown length much shorter 6.6 (6.3–6.9) 6 v. 7.8.

The Tanimbar *Melomys* is difficult to confuse with *M. rufescens* from which it differs in having a dark brown dorsum and White cheeks rather than a generally brightly coloured Cinnamon dorsum (except for *M. r. stalkeri*) with no white cheek patches; tail with flat scales rather than scales with raised granules or humps; fewer tail scales per cm 12–14 v. 16–19; and molar row generally longer, >6.3 [only *M. r. rufescens* exceeds this but then only occasionally 6.1 (5.5–6.5) 25 (from Rümmler 1938)]. Comparison with a series of *M. rufescens* from the nearest population to Yamdena Island (Wokam Island, Aru group) indicates that *M. cooperae* also differs from this form by having a narrower rostrum; incisor more opisthodont; anterior palatal foramen larger; bulla longer and more inflated, least interorbital breadth larger; and temporal ridges less pronounced.

Etymology

Named after Mrs Norah Cooper in recognition of her work in the mammal section of the Western Australian Museum. In particular for her support and contribution to the Indonesian project between 1987–1993, where she participated in the Sumba Island expedition.

OTHER SPECIMENS EXAMINED

Melomys leucogaster latipes

Australian Museum No. (AM) M13781, A ♀, skin and skull, Naiya Village, E. side Mt Karimui, S. Simbu Province, Papua New Guinea; AM 13815, A ♂, skin and skull, 2.5 km SSW Yuro Village, E. side Mt Karimui, S. Simbu Province, Papua New Guinea.

Melomys rufescens

Western Australian Museum No. (WAM) M42626–7, M42637, M42446, M42450, M42566, 4 ♂ ♂ 2 ♀ ♀, Kampung Karangguli, Wokam Island, Aru Group., Indonesia.

ACKNOWLEDGEMENTS

We are grateful for the support of both Mr J.L. Bannister, Director of the Western Australian

Museum at the time of the expedition, now retired, the Director of the Museum Zoologicum Bogoriense, Bapak M. Amir and to the Indonesian Institute of Science (LIPI), particularly Dr Soetikno, who sponsored the field work.

Thanks also to our colleagues Dr Richard How and Mr Ron Johnstone, Western Australian Museum, for their support and good company in the field. Mrs Anne Nevin typed the manuscript. Dr Tim Flannery, Australian Museum, Sydney, and Dr Chris Smeenk, Natuurhistorisch Museum, Leiden, kindly loaned reference specimens.

Dr Ken Aplin, Western Australian Museum, and Dr J. Menzies, University of Papua New Guinea offered constructive advice to improve the description of the new species.

Expedition costs were defrayed by grants to Dr D. Kitchener from: National Geographic Society, Washington and the Australian National Parks and Wildlife Service, Canberra and to Drs L. Schmitt, D. Kitchener and R. How from the Australian Research Council, Canberra. Garuda Indonesia kindly defrayed freight costs of the expeditions.

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Manuscript received 14 November 1993; accepted 5 May 1994.

Metallography and thermo-mechanical treatment of the Veevers (IIAB) crater-forming iron meteorite

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Abstract — Thirty six fragments of iron meteorite (group IIAB – Wasson *et al.* 1989) totalling 298.1 g found at Veevers crater in Western Australia (22°58'06"S, 125°22'07"E) represent the disrupted remnants of the crater-forming projectile, and confirm an origin for the ca. 75 m crater by meteorite impact. The morphology and metallography of the residual material show that the impacting meteorite was a coarsest octahedrite with a kamacite bandwidth of > 8.6 mm. Disruption of the meteorite during impact probably occurred along the grain localities of α -kamacite crystals in the original octahedral structure, but may also have resulted from failure related to intense shear deformation. Further disintegration of the surviving fragments may have occurred as the result of prolonged terrestrial weathering. Thermo-mechanical alteration of the micro-structure of the meteorite as a result of impact includes transient, localised re-heating to >800°C, shearing and plastic deformation. Failure of parts of the meteorite along brittle-cracking paths, such as crystal boundaries, may have absorbed some of the energy of terrestrial impact and allowed portions of the original micro-structure of the meteorite to be preserved. Veevers is the only known group IIAB iron associated with an impact crater.

INTRODUCTION

In Australia there are five meteorite impact craters (Wolfe Creek, Dalgarranga, Henbury, Boxhole and Veevers) with associated meteoritic fragments representing the remnants of the impacting projectiles. Of these, Veevers crater is the most recently recognised and the least well described. Veevers meteorite impact crater is situated between the Great Sandy and Gibson Deserts in Western Australia at co-ordinates 22°58'06"S, 125°22'07"E. The bowl-shaped, circular structure, measuring 70–80 m in diameter and 7 m deep, was recognised as a possible impact crater in July 1975 (Yeates *et al.* 1976). Yeates *et al.* (1976) surveyed the crater but did not find any meteoritic material that would have provided conclusive evidence of an origin by meteorite impact. Subsequently, in August 1984, two of us (EMS and CSS) visited the locality and recovered several small fragments of iron meteorite from two localities immediately to the north of the crater (Figure 1). The material (Table 1– WAM 13645–46) comprises several irregular, weathered fragments, the largest weighing 8.9 g. In July 1986, during a further visit to carry out a detailed survey of the crater (Shoemaker and Shoemaker 1988), an additional 32 metallic slugs and fragments of

meteoritic iron were recovered, the largest weighing 36.3 g (Graham 1989) (see Table 1). Most of this material was found just to the east of the crater, on the flanks of the crater rim and adjacent plain (Figure 1). A precise age for the crater has not yet been published, although Shoemaker and Shoemaker (1988) estimated that it was formed around 4000 years ago.

More recently, Wasson *et al.* (1989) analysed the meteorite and have shown it to be a normal member of chemical group IIAB containing 5.82 wt% Ni, 57.7 $\mu\text{g/g}$ Ga, 160 $\mu\text{g/g}$ Ge and 0.028 $\mu\text{g/g}$ Ir. Wasson *et al.* (1989) also suggested that the size of the recovered fragments reflects separation of cm-thick kamacite lamellae as the result of weathering or impact fragmentation. In this paper, a detailed metallographic description of the meteorite is provided, and the disruptive thermo-mechanical history of the meteorite during crater-forming impact is interpreted.

PHYSICAL DESCRIPTION AND SAMPLE PREPARATION

The weights and dimensions of the meteorite fragments recovered from the vicinity of Veevers crater are listed in Table 1 and shown (WAM

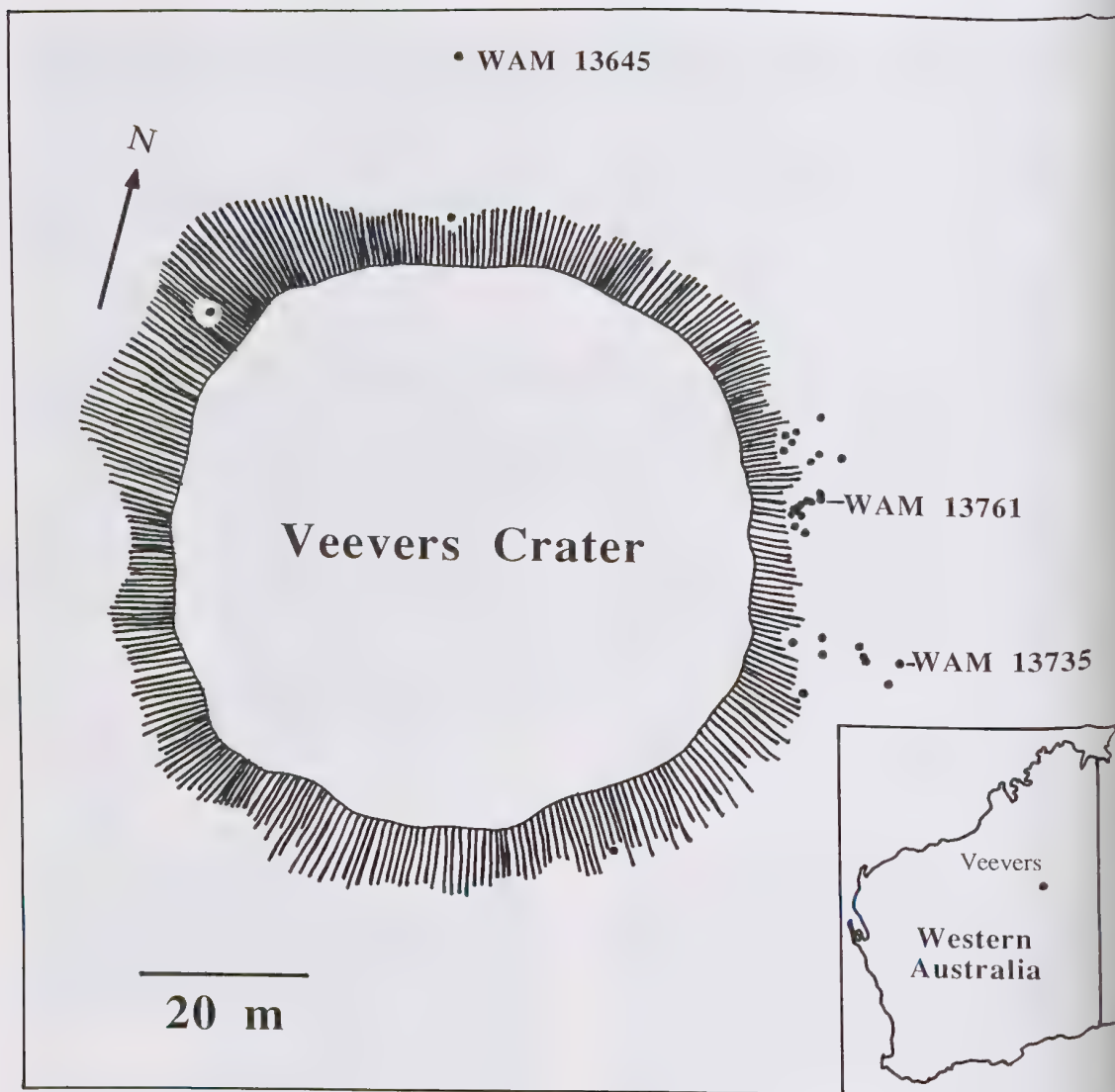


Figure 1 Location of Veevers crater and schematic map showing the distribution of meteorite fragments found by E.M. and C.S. Shoemaker.

13731–13762) in Figure 2. Fragments are weathered and possess variably thick (up to 1mm) rinds of terrestrial corrosion products around fresh metal. The total weight of the fragments is 298.1 g; individual fragments range in weight from < 0.1–36.3 g with a mass distribution skewed towards fragments in the range 2 – 8 g (Figure 3b). Fragments weighing more than 3 g are generally elongate and flattened in shape; the ratios (L/T) of their lengths (L) to maximum thicknesses (T) average 3 and range from 1.6 – 6.5. Fragments weighing more than 3 g have a mean thickness of 8.6 mm (Figure 3a).

Two fragments, one found to the north (WAM

13645) and one found to the east (WAM 13761) of the crater, were cut along their long axes, then polished and micro-etched with 2% nital for metallographic examination. An additional, irregularly shaped fragment (WAM 13735), also found to the east of the crater, was cut perpendicular to a suspected grain boundary.

METALLOGRAPHY AND STRUCTURAL CLASSIFICATION

Microscopically, the fragments examined are composed essentially of single crystals of α -FeNi (kamacite) that have been partially or completely

Table 1 Numbers, weights and dimensions of iron meteorite fragments found at Veevers impact crater

Field No.	WAM No.	weight (g)	length L (mm)	max.thickness T (mm)
VC-1-84	13645	8.9	17.9	11.4
VC-4-84	13646.1	4	32.9	5.05
VC-4-84	13646.2	2.2	23.9	4.6
VC-4-84	13646.3	<0.1	(fragments)	
VC-1-86	13731	6.9	26.75	8.05
VC-2-86	13732	2.5	20.4	5.75
VC-3-86	13733	1.8	15.7	4.9
VC-4-86	13734	12.4	20.3	9.2
VC-5-86	13735	13.9	33.1	9.3
VC-6-86	13736	4.5	27.3	6.5
VC-7-86	13737	9.3	25.5	8.9
VC-8-86	13738	3.9	16.05	8.25
VC-9-86	13739	6	20.6	8.55
VC-10-86	13740	1.3	21.15	4.6
VC-11-86	13741	8.5	24.8	8.9
VC-12-86	13742	4.7	20.35	8.45
VC-13-86	13743	13.8	30.35	11.1
VC-14-86	13744	18	26.95	12.95
VC-15-86	13745	12.2	34.7	7.3
VC-16-86	13746	1.9	15.85	4.4
VC-17-86	13747	17.8	24.35	12.95
VC-18-86	13748	2.8	17.75	5.2
VC-19-86	13749	7.7	19.45	7.8
VC-20-86	13750	2.3	15.85	5.6
VC-21-86	13751	1.3	(small fragments)	
VC-22-86	13752	26.6	(specimen used for terrestrial age determination)	
VC-23-86	13753	4.7	15.65	7.0
VC-24-86	13754	4.9	17.5	8.75
VC-25-86	13755	6.2	21.75	7.8
VC-26-86	13756	5	19.5	7.2
VC-27-86	13757	4.8	19.0	6.75
VC-28-86	13758	4.6	17.1	8.1
VC-29-86	13759	6.6	22.0	6.05
VC-30-86	13760	19.1	36.0	11.3
VC-31-86	13761	36.3	31.35	15.4
VC-32-86	13762	10.6	26.8	8.3

transformed to unequilibrated, ragged α_2 -kamacite similar to that found in the heat affected zones of freshly fallen irons. Metal in the fragments WAM 13761 (36.3 g) and WAM 13735 (13.9 g) found to the east of the crater shows complete transformation to coarse (10-200 μm units), ragged α_2 , whereas the largest fragment (WAM 13645 – 8.9 g) found to the north of the crater is only partially transformed to finer grained (5–50 μm) α_2 units, mainly along zones of intense shear deformation.

One fragment (WAM 13761) displays several mm-sized inclusions of schreibersite [(FeNi)₃P], and both fragments examined contain abundant rhabdites (prismatic crystals of schreibersite). In all fragments examined, schreibersite crystals and rhabdites are kinked, kneaded and deformed, and their grain boundaries show incipient reaction haloes with the surrounding metal (Figure 4a). Evidence of shock-melting in Veevers is sparse. However, where shear-zones intersect large

crystals of schreibersite, small (< 20 μm) cloudy, wedge-shaped pools of shock-melted phosphide have been generated that penetrate the phosphide from the phosphide-metal interface. Additionally, some rhabdites have been smeared out and melted along zones of shear deformation.

Portions of fragment WAM 13645 that have not been transformed to α_2 show deep-seated Neumann bands (mechanical shock-twins) that are degenerated (Figure 4b), and sub-grain boundaries that are decorated with rhabdites. The fragments have been plastically deformed and the metal is traversed by a few intense zones (<1 mm wide) of shear deformation characterized by sub-microscopic recrystallization. Locally, terrestrial corrosion has penetrated along cracks developed in the shear-zones making them visible to the naked eye. Several shear-zones run parallel with, and close to, the outer surfaces of the fragments. In the fragment from north of the crater, three sets of



Figure 2 Fragments of the Veevers meteorite (WAM 13731-13762) recovered from the area to the east of the crater (see Figure 1).

shear-zones are evident that intersect at *ca.* 60° and some shear-zones have been propagated along pre-existing Neumann bands. In the fragment WAM 13761, in addition to zones of shear deformation, there are occasional diffuse, sinuous lines of stained metal that do not appear to be associated with plastic deformation. One such sinuous line is cut and displaced by a shear-zone indicating that the structure from which it was formed pre-dates plastic deformation of the metal (Figure 4c). The displacement of the structure indicates that the throw of the shear zone is *ca.* 400 μm .

The suspected grain boundary in fragment WAM 13735 is heavily invaded with terrestrial corrosion products that have masked the original structure. Vestiges of troilite occur and, locally, terrestrial oxides pseudomorph a pre-existing eutectic-like structure. Other minerals observed in the unaltered portions of Veevers fragments include carlsbergite (CrN) and an unidentified, partially resorbed mineral (Figure 4b), probably roaldite ($[\text{Fe,Ni}]_3\text{N}$) (Nielsen and Buchwald 1981), the latter occurring

rarely as narrow (1–2 μm), long (up to 1.2 mm) lamellae. Neither $\gamma\text{-FeNi}$ (taenite), nor shock-hardened $\epsilon\text{-kamacite}$ transformations were observed.

Structural classification

All previously described irons belonging to chemical sub-group IIB with Ni contents in the range 5.5–6.9 wt % are structurally coarsest octahedrites (Ogg) with $\alpha\text{-kamacite}$ bandwidths >3.3 mm (Buchwald 1975). Disruption of the Veevers projectile during impact has destroyed the original macro-structure of the meteorite. However, the nature of the surviving fragments gives some indication of the original structure of the meteorite. The shape and mineralogy of the fragments show that, predominantly, the structure of the meteorite comprised irregular, stubby lamellae of kamacite (L/T c.1.6–6.5). From their plate-like morphology, it follows that the maximum thicknesses of the surviving fragments are likely to approximate to the kamacite

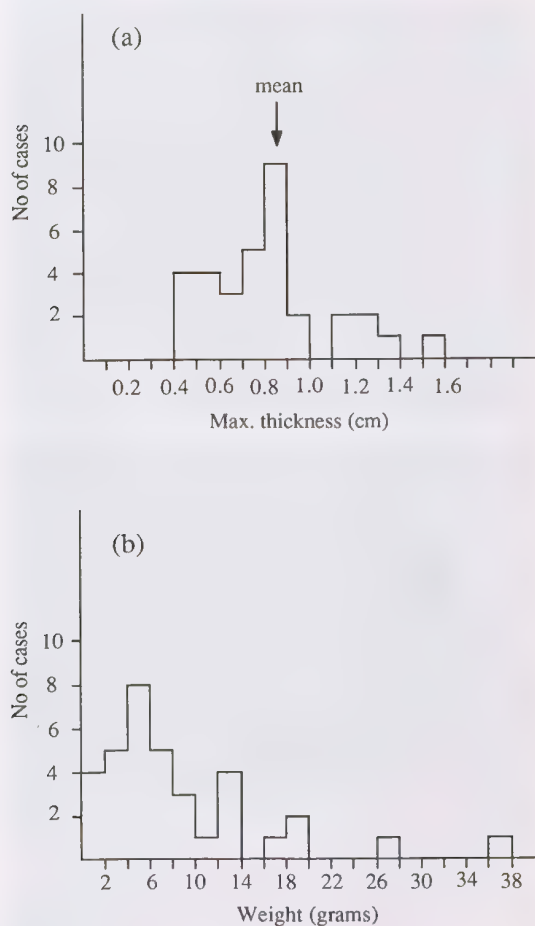


Figure 3 Dimensional and mass analysis of meteorite fragments found at Veevers crater; (a) fragment thickness frequency, (b) mass frequency.

bandwidth of the original octahedral structure. The average thickness of fragments > 3 g is 8.6 mm (Figure 3a), whereas the average thickness of fragments > 5 g is 9.6 mm. These dimensions indicate a coarsest octahedral (Ogg) structure, and correspond well with the bandwidths (9–10 mm) of other group IIAB irons with similar Ni contents (ca. 5.8 wt%) that have been described (Buchwald 1975).

Group IIAB irons with bulk Ni contents greater than 5.5 wt% frequently contain some residual γ -taenite or plessite ($\alpha + \gamma$) (Buchwald, 1975). The frequency of taenite or plessite fields in these meteorites rarely exceeds one in sectional areas ranging from 10–25 cm². The bulk Ni content (5.82 wt%) of Veevers (Wasson *et al.* 1989) suggests that some residual γ -taenite should be present in the meteorite. In the small sectional area of the residual fragments of Veevers examined (< 4 cm²) no taenite

or plessite was encountered. However, it is likely that the undisrupted Veevers meteorite contained residual taenite.

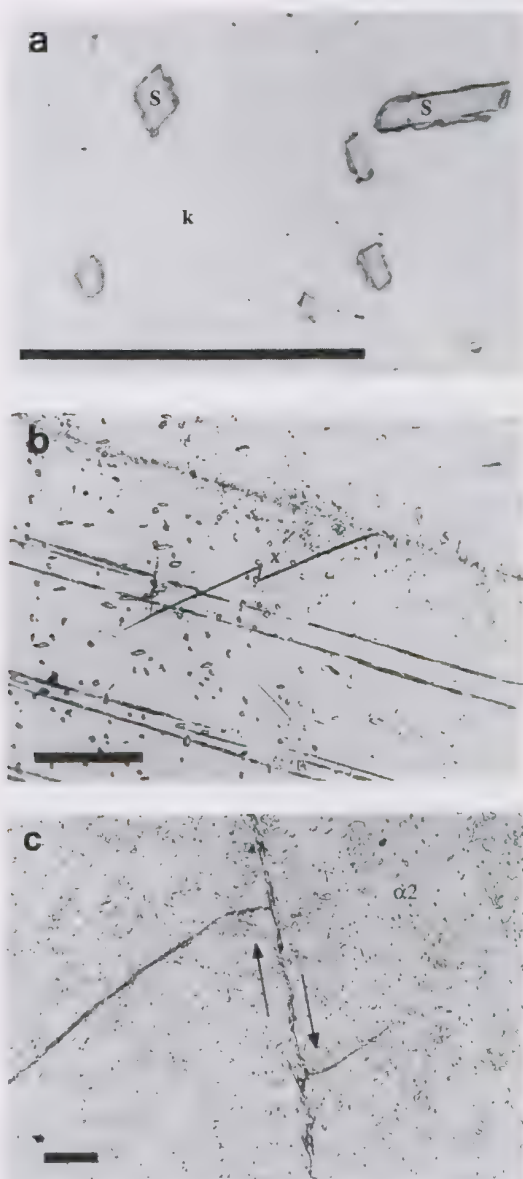


Figure 4 Details of the microstructure of Veevers meteorite fragments. (a) Schreibersite [s] showing incipient reaction haloes with surrounding kamacite [k]. (b) Kamacite containing abundant rhabdites, degenerated Neumann bands and lamellae of an unidentified mineral [x], probably roaldite. (c) Sinuous line of stained metal (probably decomposed roaldite) cut and translated by a zone of shear deformation (arrowed). Surrounding metal transformed to ragged α_2 -kamacite. Scale bars 100 μ m (2% nital etch).

DISCUSSION

In Veevers fragments, transformation of kamacite to ragged α_2 indicates a transient, but severe re-heating to temperatures above the α to γ transformation temperature, followed by rapid cooling (Brentnall and Axon 1962; Axon *et al.* 1968; Lipschutz 1968). Reaction haloes between schreibersite and metal indicate incipient resorption of the phosphide and are also consistent with a brief, but severe re-heating event. This re-heating event is superimposed on earlier formed structures in Veevers and appears to be the most recent thermal event in the history of the meteorite. There are several possible explanations for the cause of the re-heating in Veevers that include; pre-terrestrial cosmic shock reheating, frictional heating during atmospheric passage, shock reheating on impact, and contact with hot impact ejecta. However, there are a number of significant features of the microstructure of Veevers indicating that the observed effects of transient re-heating were associated with the impact event.

As shown for Canyon Diablo by Heymann *et al.* (1966), the localised occurrence of severe thermal effects observed in the interiors of some of the Veevers fragments indicates steep temperature gradients that exclude conductive heating (e.g., atmospheric passage and contact with hot ejecta) as a mechanism for re-heating. In Veevers, the superimposition of thermal alteration on earlier structures, and its clear association in at least one fragment with intense shear deformation, suggests that heating in that case was caused by shock-loading during the formation of the crater and the disruption of the impacting projectile. However, in the largest fragment recovered (WAM 13761) the general transformation of metal to α_2 -kamacite that is not obviously associated with mechanical deformation does not exclude the possibility of conductive re-heating. Notwithstanding, the similarity of the condition of the schreibersite and rhabdites in all three fragments examined is consistent with re-heating for short (seconds) duration rather than prolonged (minutes/hours) heat-treatment in a hot ejecta blanket.

Comparison with experimentally heated and shock re-heated samples of iron meteorite allows the magnitude and duration of thermo-mechanical treatment of Veevers to be determined more accurately. The thermal effects observed in kamacite and schreibersite in lightly shocked samples of Canyon Diablo experimentally heat-treated in air for 10 and 100 seconds at 800–850 °C (Figure 5a and b) and allowed to cool by radiation are very similar to the range of structures observed in Veevers fragments. In these samples, metal is partially or wholly transformed to α_2 -kamacite comprising 10–200 μm units, and

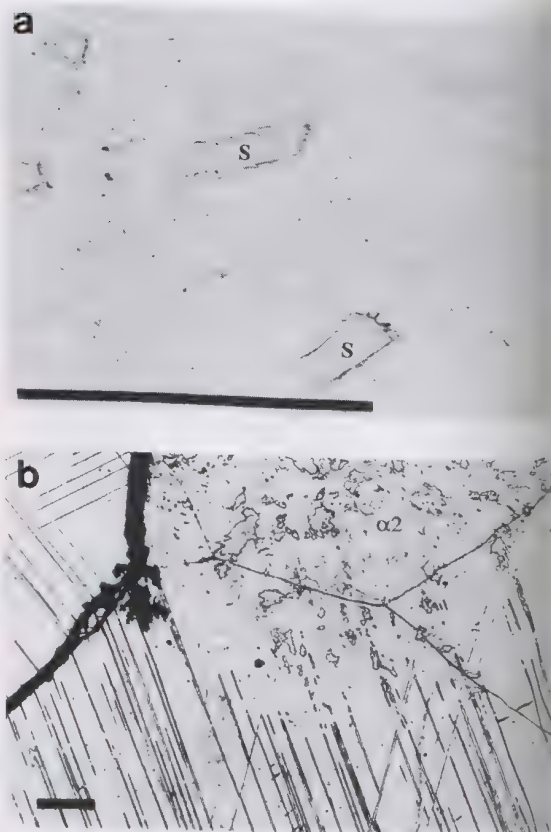


Figure 5 Samples of the IAB iron, Canyon Diablo, experimentally heated in air for (a) 100 secs at 800°C and (b) 10 secs at 850°C. Note incipient reaction schreibersite [s] with surrounding metal, degenerated Neumann bands and α_2 transformations. Scale bars 100 μm (2% nital etch).

phosphides show incipient, ragged reaction haloes with surrounding metal. In samples heated to the same temperatures but for longer (100–1000 secs) periods, the reaction haloes around phosphides become more prominent, and thorn-like protuberances penetrate the metal from the phosphide metal interface. These features were not observed in the Veevers fragments examined.

The peak temperature to which Veevers fragments were subjected during terrestrial impact is more difficult to determine. Samples of Canyon Diablo experimentally heated to 1000°C for short duration (300 secs) by Brentnall and Axon (1962) showed extensive eutectic melting and resorption of schreibersite. Widespread melting of schreibersite was not observed in the Veevers fragments examined, suggesting that overall re-heating of the surviving fragments was considerably less than 1000°C. However, 10

account for the isolated areas of incipiently melted schreibersite, attenuation of shock waves at grain boundaries and shearing could have generated localised 'hot spots' where temperatures may have approached 1000°C. Incipient melting of schreibersite at grain boundaries as the result of intense shear deformation observed in Veevers is identical to that described by Axon *et al.* (1977) from similarly deformed phosphide inclusions in the crater-forming iron Canyon Diablo. Evidence from fragment WAM 13735 indicates that extensive shock-melting in Veevers may have occurred along those grain boundaries containing abundant troilite. Troilite has a low shock impedance relative to Fe and is known to induce high shock-temperatures even under conditions of moderate shock-loading.

The shock pressures required to produce the structural changes in Veevers fragments can be inferred from the estimated residual temperatures indicated by the thermal alteration of minerals in the meteorite. The relationship between shock pressure and residual temperature for pure iron has been determined experimentally by McQueen *et al.* (1962) and for iron meteorite material by Heymann *et al.* (1966). In shocked iron meteorites, extensive or complete transformation to α_2 -kamacite occurs at applied pressures in the range 0.8–1 Mb (Heymann *et al.* 1966). In specimens of the Odessa meteorite shocked to pressures in this range, Heymann *et al.* (1966) also noted that small patches of shock-hardened ϵ -kamacite may occur once in sectional areas up to 20 cm². The apparent absence of ϵ -kamacite in Veevers may simply be a function of the small sectional area of the meteorite examined.

As suggested by Wasson *et al.* (1989), the plate-like morphology of the surviving fragments of Veevers indicates that the meteorite broke up during impact predominantly along α - α crystal boundaries in the original octahedral structure. Large crystals of schreibersite, such as that observed in Veevers fragment WAM 13761, also provide brittle-cracking paths that could have facilitated break-up. From a study of shrapnel-like fragments of the Henbury crater-forming iron, Axon and Steele-Perkins (1975) have suggested that fracturing of that meteorite took place along surfaces of shear-faulting generated during impact. Parting along zones of shear displacement may have provided an additional mechanism of failure in the Veevers meteorite, and this is supported by the occurrence of shear-zones that parallel the outer surfaces of the fragments. The angles of intersection (*ca.* 60°) of some of the shear-zones in Veevers coincides with the angles between the (111) directions of kamacite in the octahedral structure of iron meteorites. It is possible that the habit planes of the octahedral structure and other

cubic planes in Veevers influenced the shearing forces generated by impact. Subsequently, the penetration of terrestrial oxidation along grain boundaries and shear-zones may have led to further disintegration of the surviving fragments, as suggested by Wasson *et al.* (1989).

Much of the pre-terrestrial micro-structure of Veevers has been destroyed or modified as the result of thermo-mechanical alteration during crater-forming impact. Nevertheless, portions of the original micro-structure of the meteorite have been preserved. The observed Neumann bands that have been plastically deformed and partially degenerated by re-heating appear to pre-date terrestrial impact. The sinuous lines of stained metal observed in fragment WAM 13761 are interpreted as the resorped lamellae of an as yet unidentified mineral, probably roaldite.

Comparison with other crater-forming irons

Out of the twelve other crater-forming irons known (Grieve 1991), the most extensively studied are Canyon Diablo (IAB), Odessa (IAB) and Henbury (IIAB) (Buchwald 1975). Canyon Diablo and Odessa are both coarse octahedrites, whereas Henbury is a medium octahedrite. All three meteorites are associated with craters that are very much larger than Veevers. In the case of Henbury, the impact resulted in some thirteen craters including several that are of similar size to Veevers. Structural variations between the crater-forming irons and differences in the magnitude of their impacting events have resulted in an enormous range of shock-induced features in the surviving fragments. Notwithstanding, there are strong similarities in the overall nature of thermo-mechanical alteration and mechanism of disruption suffered by many crater-forming irons.

In terms of crater size, the closest analogue to Veevers is the largest of a group of nine craters at Kaalijärv, located on Saaremaa Island, Estonia (Buchwald 1975). The largest crater measures 110 m in diameter and eight smaller craters vary from 12–40 m in diameter (Tiirmaa 1992). Kaalijärv is a coarse octahedrite (IAB) and the material recovered from the craters comprises small slugs of metal generally less than 20 g in weight (Buchwald 1975). Metallographically, the Kaalijärv meteorite shows shock hardening, shear deformation and localised recrystallization of metal. Overall, the thermal alteration of Kaalijärv fragments is less than those observed in Veevers fragments and is generally confined to zones of shear deformation.

The IIAB iron Sikhote-Alin, that fell in eastern Siberia in 1947, is the largest known shower in historical times and is structurally and chemically similar to Veevers. Some 23.2 tons of fragmental material were recovered from a large strewnfield covering 1.6 sq. km and including 122 impact

holes (Krinov 1963; Buchwald 1975 – and references therein). Many of the masses of Sikhote-Alin broke up during impact and some of the recovered fragments display the earliest stages of shock-metamorphism. Buchwald (1975) noted that many of the disrupted fragments showed octahedral parting, and that fissures are well developed along kamacite grain boundaries that are loaded with schreibersite. However, more intensely deformed fragments also show shear deformation and visibly distorted zones near their surfaces. In addition, Buchwald (1975) noted that fissures had also developed along the cubic cleavage planes of kamacite lamellae in Sikhote-Alin, although these appeared to have played a minor rôle during the fragmentation of the impacting masses.

Although of much less intensity, the style of thermo-mechanical impact alteration displayed by both the Sikhote-Alin and Kaalijärvi meteorites is very similar to that observed in Veevers fragments.

SUMMARY AND CONCLUSIONS

Veevers is the only known crater-forming iron of chemical group IIAB. Sub-group IIB irons are rare, accounting for only 4% of all iron meteorites, and less than 0.5% of all meteorites. The association of an unusual meteorite type with an impact crater is especially significant. Dry conditions and extremely low erosion rates in the arid zone of Australia over at least the last 4000 years account for the excellent state of preservation of both the crater and the surviving fragments of meteorite.

The metallography of the surviving fragments of Veevers shows that the meteorite was subjected to a pre-terrestrial history of mild shock-loading of a thoroughly annealed structure that resulted in at least one generation of Neumann band deformation. Subsequently, terrestrial impact caused intense shock-loading of the meteorite that resulted in shearing and plastic deformation with attendant localised heating to $>800^{\circ}\text{C}$. In accommodating the complex pattern of shock waves generated by high-velocity impact with the Earth, a portion of the meteorite was disrupted mainly along kamacite crystal boundaries in the original coarsest (> 8.6 mm) octahedral structure. Failure may also have occurred as the result of fracturing along zones of intense shear-deformation that may, in turn, have been influenced by the octahedral structure of the meteorite. As a result of the disruption of a portion of the projectile along brittle-cracking paths some of the energy of the impact event may have been absorbed, allowing portions of the original microstructure of the meteorite to be preserved.

Most of the remains of the meteorite may be mixed widely with the breccia under the crater

floor. A subordinate fraction of the meteorite was broadly sprayed out of the crater and is now buried beneath the surrounding sand sheet. Subsequently, terrestrial weathering has corroded the fragments and may also have contributed to further disintegration. However, because of prolonged aridity in the desert region where the crater occurs, rusting is not extensive and the fragments retain large cores of fresh metal. The close approximation of the average thickness of fragments (8.6 mm) to the bandwidths (9–10 mm) of other IIAB irons of similar Ni content suggests that corrosional losses due to weathering were unlikely to have been greater than 1–2 mm. A thorough search of a wide area around the crater may yield larger fragments of Veevers that became detached from the projectile during atmospheric flight, and that were not involved in the cratering event.

ACKNOWLEDGEMENTS

The authors thank the late Dr H. J. Axon for providing experimentally heat-treated samples of Canyon Diablo for study. Assistance in the preparation of the Veevers fragments was generously provided by the Electron Microscope Centre of the University of Western Australia, through Dr B. J. Griffin. Professor J. T. Wasson and Dr V. F. Buchwald are thanked for their helpful reviews.

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Manuscript received 21 February 1994; accepted 8 July 1994.

Morphological variation in *Pteropus lombocensis* (Chiroptera: Pteropodidae) in Nusa Tenggara, Indonesia

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Abstract – Recent terrestrial vertebrate faunal surveys in Nusa Tenggara, Indonesia, collected specimens of *Pteropus lombocensis* from islands from which the species had not previously been reported (Sumbawa, Lombok and Pantar), as well as from Lombok, Flores and Alor Islands.

A univariate and multivariate statistical analysis of 28 morphological (skull dentary, dental and external) characters showed that adult *P. lombocensis* was not sexually dimorphic, but that significant variation occurred, particularly in dental characters, between the island populations.

Two subspecies are recognised in *P. lombocensis*. These are the western form, *P. l. lombocensis* Dobson, 1878 (Lombok and Sumbawa Islands), and the eastern form, *P. l. heudei* Matschie, 1899 (Flores, Lombok, Pantar and Alor).

INTRODUCTION

Andersen (1912) stated that the members of the *Pteropus lombocensis* group were characterised by their small size (forearm length 94–127 mm); short and broad rostrum; conspicuously reduced M_3 , M^2 and I_1 ; I_1 , one-quarter to one-sixth the bulk of I_2 ; ears moderate or short; tibia furred dorsally, except in the species from the Caroline Islands; hair pale or dark brown dorsally with a buffy mantle, except in the Caroline Islands species which is a darker brown.

Andersen (1912) recognised two species from the *P. lombocensis* group in Indonesia; these were both restricted to Nusa Tenggara. They were *P. lombocensis* Dobson, 1878 (Lombok Island – the type locality and Flores Island) and *P. solitarius* K. Andersen, 1908 (Alor Island). The form *P. heudei* Matschie, 1899 from Flores Island, was originally described by Heude (1896) as *P. tricolor* but this name was preoccupied. Andersen (1912) and Hill in Corbet and Hill (1992) considered *P. heudei* synonymous with *P. lombocensis*. Hill (*op cit.*) also considered *P. solitarius* a subspecies of *P. lombocensis*.

A series of terrestrial vertebrate surveys throughout islands in southern Indonesia between 1987 and 1993 by staff from both the Western Australian Museum and Museum Zoologicum Bogoriense, resulted in the collection of a series of *P. lombocensis* from Lombok, Sumbawa, Flores, Lombok, Pantar and Alor islands. This is a much more extensive series of specimens than was hitherto available for study. They are also the first records of the species from Sumbawa, Lombok and Pantar islands.

This paper reports on an examination of morphological variation among island populations of *P. lombocensis* and evaluates this variation in the context of their subspecific taxonomy.

MATERIALS AND METHODS

A total of 30 adult specimens (listed in specimens examined section) was examined. These were from Lombok Island (8♂♂, 3♀♀); Flores Island (1♂, 1♀); Lombok Island (2♂♂, 6♀♀); Pantar Island (4♀♀) and Alor Island (2♂♂, 3♀♀). Additionally four subadult specimens were examined from Sumbawa Island. The localities of these specimens are shown in Figure 1. All specimens are currently lodged in the Western Australian Museum.

Eighteen measurements of skull, dentary and dental characters and 10 of external body characters (all in mm) were recorded from adult specimens.

The measurements recorded were GSL, greatest skull length; CBL, condylobasal length; PL, palatal length; MFW, mesopterygoid fossa breadth; RL, rostrum length, from anteriormost internal margin of orbit to posterior margin of nares; IOB, minimum interorbital breadth; ZW, zygomatic width; BB, braincase breadth above zygoma; DL, dentary length; C¹C¹, width across C¹ to C¹ from the labial side at alveoli; P⁴P⁴, palatal breadth measured between posterior upper premolars; M¹M¹, width across M¹ to M¹ from the labial side at alveoli; C¹M², upper maxillary tooth row length; C₁M₃, lower canine to M₃ length; P³L, middle upper premolar crown length; P³B, middle upper premolar crown breadth; M¹L, first upper premolar

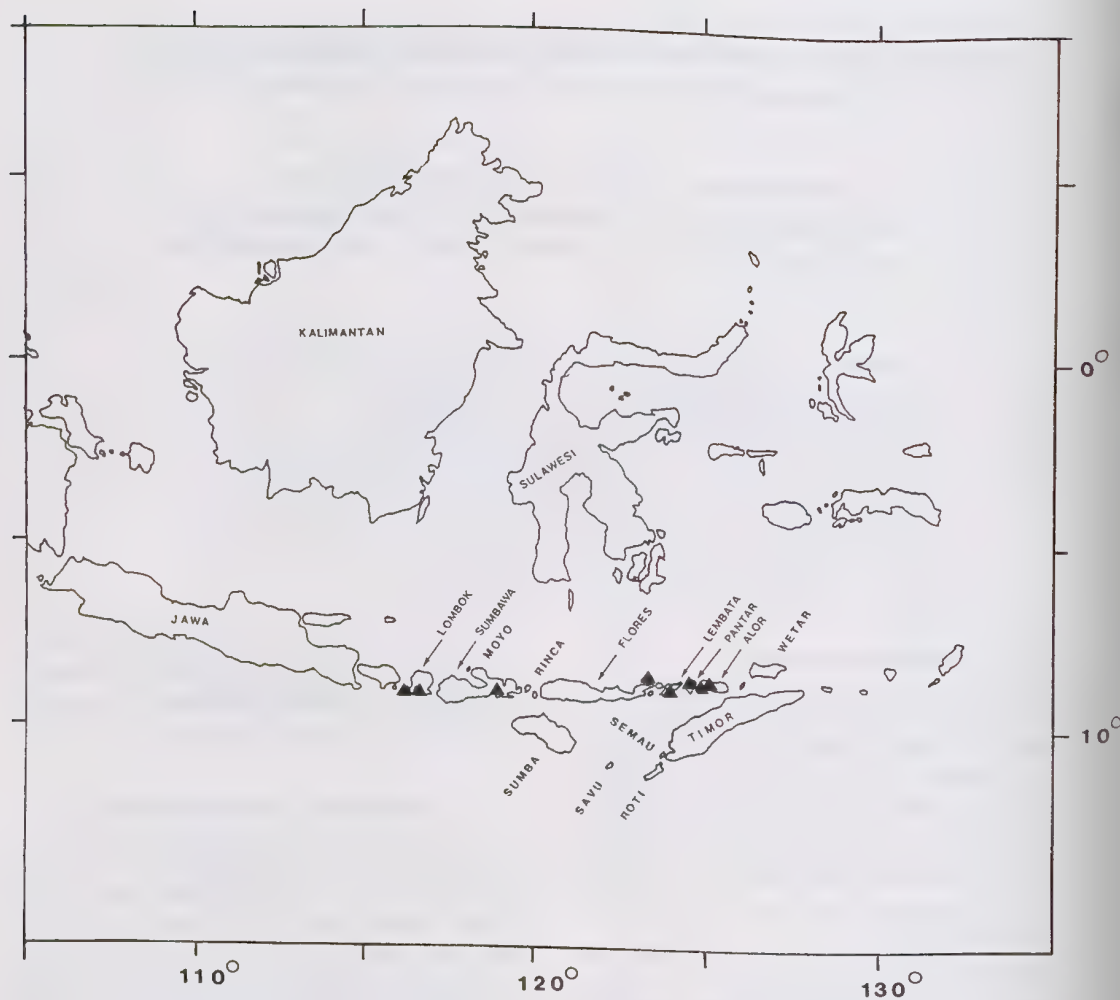


Figure 1 Locality of *Pteropus lombocensis* used in this study.

Table 1 Measurements, in mm, for skull, dentary, dental and external body characters (see Materials and Methods section for explanation of character codes) of adult *Pteropus lombocensis lombocensis* (Lombok Island) and *P. lombocensis heudei* (Flores, Lembata, Pantar and Alor Islands). N, sample size; \bar{X} , mean; SD, standard deviation, MIN, minimum; and MAX, maximum.

		GSL	CBL	PL	MFW	RL	IOB	ZW	BB	DL	C'C'	P'P'	M'M'	C'M'
<i>P. l. lombocensis</i> Lombok I.	N	11	11	11	11	11	11	11	11	11	11	11	11	11
	\bar{X}	55.03	53.11	29.73	6.98	14.58	8.08	30.24	21.12	41.91	10.63	9.54	15.61	20.06
	SD	0.99	0.89	0.73	0.23	0.51	0.38	0.59	0.49	0.75	0.33	0.36	0.67	0.40
	MIN	53.18	51.23	28.22	6.60	13.72	7.36	29.43	20.30	40.28	10.13	8.82	14.26	19.16
	MAX	56.98	54.22	31.06	7.29	15.38	8.79	31.02	21.82	43.09	11.07	10.01	16.89	20.58
<i>P. l. heudei</i> Flores-Lembata -Pantar-Alor	N	18	18	18	18	18	18	18	18	18	18	18	18	18
	\bar{X}	54.09	52.03	29.14	7.09	14.30	7.87	29.79	20.91	40.62	10.40	9.51	15.05	19.28
	SD	1.05	1.15	0.70	0.35	0.57	0.22	0.72	0.43	0.85	0.31	0.34	0.30	0.32
	MIN	52.35	50.06	27.97	6.65	13.34	7.47	28.21	19.97	38.93	9.89	8.91	14.45	18.82
	MAX	55.83	53.69	30.36	7.88	15.25	8.33	30.90	21.65	41.85	10.95	10.20	15.57	19.88

crown length; M¹B, first upper premolar crown breadth; FA, forearm length; D2M, digit 2 metacarpal length; D3M, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4M, digit 4 metacarpal length; D5M, digit 5 metacarpal length; TIB, tibia length; PES, pes length; EAR, ear length.

The skull, dentary and dental characters were measured to 0.01 an accuracy of mm, while the external characters were measured to 0.1 mm. Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital-basisphenoid, basisphenoid-presphenoid and palatine-maxillary.

The effect of sex and island on all characters was examined by standard multiple regressions (where all effects were assessed simultaneously) for those islands for which we had specimens of both sex. Pantar Island was excluded because we had only female specimens from that island.

Stepwise canonical variate (discriminant function) analyses (DFA) were run for skull, dentary, dental and external body characters using all characters measured, except for tibia length [because it had a significant interaction ($P<0.01$) between island and sex], for males and females combined.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island are presented in Table 1 for all characters measured.

Multiple regressions

Multiple regressions were run for skull, dentary and external characters on four islands (Lombok, Flores, Lembata and Alor). The results of this

analysis are presented in Table 2. Because of the number of interactions being tested some of these tests may be significant by chance alone at $0.05 > P > 0.01$. Consequently, significance levels for this analysis were set at $P<0.01$.

Sex

No characters were significantly influenced by sex alone, but there was a significant ($F_{3,17} = 6.046$; $P = 0.005$) interaction between sex and island for tibia length. This interaction resulted from the tibia length for the male being much longer than the female (56.3 *v.* 50.4) on Flores Island, whereas on the other islands they were subequal in length.

Island

Some dental measurements only were significantly influenced by island alone. These were: C¹M² length ($F_{3,17} = 10.79$, $P<0.001$); C₁M₃ length ($F_{3,17} = 44.52$, $P<0.001$); P³ breadth ($F_{3,17} = 8.94$, $P = 0.001$); and M¹ breadth ($F_{3,17} = 12.54$, $P = 0.001$).

Multivariate analysis

Because of the absence of any significant influence of sex, apart from the significant interaction between sex and island for tibia length, males and females were combined for all characters, except for tibia length, for the following DFA. Tibia length was excluded from this analysis.

The DFA was first run for the remaining 27 characters for all islands (Lombok, Flores, Lembata, Adonara, Pantar and Alor). This analysis extracted two significant functions which explained 92% of the variance (Figure 2). A total of 86.2% of individuals was correctly classified to their appropriate island. Three clusters were apparent from Figure 2. These were Lombok Island, Alor Island and a third group comprising Lembata, Flores and Pantar Islands. The DFA run on these three above groups, using all 27 characters, again extracted two significant functions that explained 100% of the variance, with 96.5% of individuals correctly classified to their appropriate group. Only

Table 1 (continued)

C ₁ M ₃	P ¹ L	P ¹ B	M ¹ L	M ¹ B	FA	D2M	D3M	D3P1	D3P2	D4M	D5M	TIB	PES	EAR
11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
22.69	3.88	2.97	5.13	2.80	117.4	57.8	80.4	54.8	81.8	80.2	84.9	52.5	29.5	26.8
0.29	0.15	0.11	0.28	0.13	2.6	1.7	2.8	1.3	1.7	2.7	2.6	1.3	0.8	0.7
22.19	3.61	2.77	4.68	2.67	113.6	55.3	76.3	52.4	77.7	75.2	81.2	50.1	28.7	25.6
23.20	4.08	3.17	5.51	3.09	121.1	60.5	85.9	56.5	84.4	85.0	90.3	54.5	31.0	27.6
18	18	18	18	18	18	18	18	18	18	18	18	18	18	18
21.09	3.81	2.74	4.82	2.53	114.6	56.2	78.9	53.2	81.9	78.5	82.9	51.2	28.9	27.5
0.54	0.16	0.11	0.33	0.10	4.3	2.2	2.5	2.3	2.6	2.9	3.1	2.3	1.0	1.0
19.28	3.53	2.51	4.20	2.29	107.4	50.9	73.2	49.2	76.3	72.3	75.6	46.4	26.5	25.9
21.87	4.14	2.92	5.36	2.64	122.0	60.1	83.4	56.1	86.2	83.9	87.7	56.3	30.2	29.5

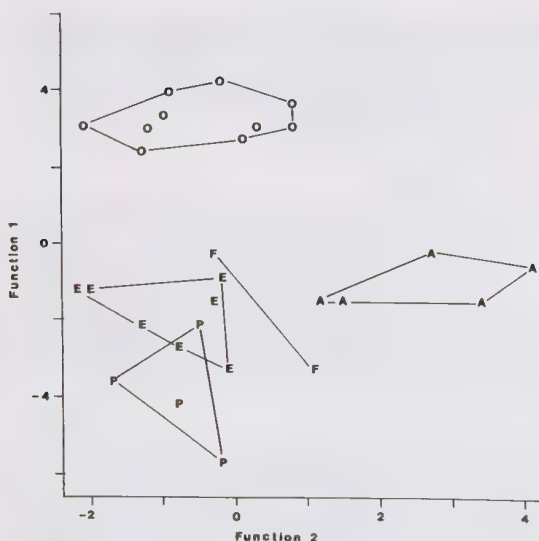


Figure 2 Plot of Functions 1 and 2 from canonical variate analysis of five island groups (Lombok, O; Flores, F; Lembata, E; Pantar, P; and Alor, A) based on 27 characters (see text), with males and females combined.

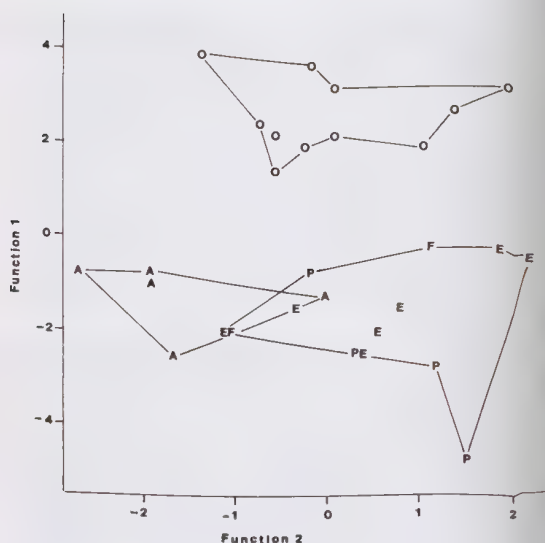


Figure 3 Plot of Functions 1 and 2 from canonical variate analysis of three island groups (Lombok, Alor and Flores-Lembata-Pantar) and a reduced set of 5 characters (see text), with males and females combined. Abbreviations for island populations as for Figure 2.

one Alor specimen was misclassified (to the Lembata-Flores-Pantar group). Because the number of characters in this latter analysis ($N = 27$) greatly exceeds the sample size of the smallest group (Alor, $N = 5$) the DFA was repeated for these three groups using a reduced set of five characters. This reduced set was selected from this latter analysis to minimise Wilk's lambda. These five characters were: C_1M_3 length, M^1 width, C^1M^2 length, rostrum length and digit 4 metacarpal length. The DFA using this reduced set of characters produced similar DFA plots to those based on the three island groups using the 27 characters. Consequently, only results based on these five characters are detailed below. This DFA extracted two significant functions that explained all the variance (Figure 3). Function 1, which explained 87.9% of the variance, separated the Lombok Island group from the other two groups. The character with the canonical discriminant function coefficient that loaded heavily (>0.5) on Function 1 was C_1M_3 length (Table 3). This suggested that this character was an important discriminant between the Lombok Island population and the other populations. Function 2, which explained 12.1% of the variance, partially separated the Alor Island population from the Flores-Lembata-Pantar population. The characters that loaded heavily (>0.5) on Function 2 were C^1M^2 length (1.02), rostrum length (0.94), digit 4 metacarpal length (0.73) and M^1 breadth (Table 3). This suggested that

a number of dental, skull and external characters were involved in the partial separation of the Alor population from the other eastern Nusa Tenggara populations. A total of 89.7% of individuals was correctly classified to their appropriate island group. The Lombok Island population was most distinct, with 100% of its individuals correctly classified. All misclassifications occurred between the Alor population and those of the other eastern islands. One of the five Alor Island individuals was misclassified to the Flores-Lembata-Pantar group, while two of the 13 individuals in this latter group were misclassified to the Alor population.

Summary of multivariate analysis

The above analysis indicates that two broad morphological forms occurred among *Pteropus lombocensis* in Nusa Tenggara. These were the Lombok Island form (*Pteropus lombocensis lombocensis*) and a form involving the remaining eastern populations (Flores, Lembata, Pantar and Alor), in which the Alor population is slightly differentiated from the others. This differentiation of the Alor form from the other eastern populations is slight and is not considered to have taxonomic significance. Of the two named forms in these eastern Nusa Tenggara islands (*P. solitarius* - Alor and *P. heudei* - Flores), *P. heudei* has priority and becomes the subspecific name (*P. lombocensis heudei*) for this eastern form.

Table 2 Multiple regressions on sex and island populations (Lombok, Flores, Lembata and Alor) of *Pteropus lombocensis* for skull, dentary, dental and external body characters. F values are presented for the main effects and their interactions. For explanation of character codes see Material and Methods section. Significance levels are *, 0.05>P>0.01; **, 0.01>P>0.001; ***, P<0.001.

CHARACTER	MAIN EFFECTS		INTERACTION SEX. ISLAND
	SEX	ISLAND	
GSL	1.319	1.455	0.079
CBL	0.750	2.082	0.064
PL	0.982	1.819	0.064
MFW	0.881	1.705	0.509
RL	0.290	0.466	0.339
IOB	2.596	0.870	0.533
ZW	0.176	0.697	1.967
BB	0.497	0.670	1.834
DL	1.582	3.028	0.581
C ¹ C ¹	1.346	0.865	1.368
P ¹ P ⁴	0.002	1.589	1.924
M ¹ M ¹	0.047	1.255	0.150
C ¹ M ²	0.044	10.788***	1.513
C ₁ M ₃	4.902*	44.522***	2.232
P ³ L	1.605	0.853	1.772
P ³ B	2.178	8.942**	0.104
M ¹ L	0.108	1.382	0.926
M ¹ B	0.997	12.537***	0.677
FA	0.003	1.846	1.544
D2M	0.020	1.436	1.334
D3M	0.020	1.266	0.515
D3P1	0.504	2.116	1.288
D3P2	0.304	0.862	2.765
D4M	0.251	1.334	1.598
D5M	0.278	1.144	1.387
TIB	1.531	4.417*	6.046**
PES	3.685	1.877	2.023
EAR	0.098	2.446	0.626
Degrees of freedom	1,17	3,17	3,17

SYSTEMATICS

Pteropus lombocensis lombocensis Dobson, 1878
Pteropus lombocensis Dobson, 1878: 34, pl. iii, fig. 2,
pl. iv, fig. 4.

Holotype
Natural History Museum, London, Number
64.4.12.2, adult male, ‘cabinet skin’ and skull.

Type locality
Lombok Island, Nusa Tenggara.

Specimens examined
Lombok Island (all adults)
Desa Pelangan, 8°48'S, 115°56 E, 1♂, WAM
M30603; Desa Kuta, 8°55'S, 116°15'E, 3♂♂ 1♀,
WAM M30611–4; Matahari Inn, Near Kuta, 4♂♂
2♀♀, WAM M(36108, 36155, 36158, 36172, 36174–
5).

Sumbawa Island (all subadults)
Desa Daha, 8°45'S, 118°26'E, 3♂♂ 1♀, WAM
M(31710–1, 31722, 31742).

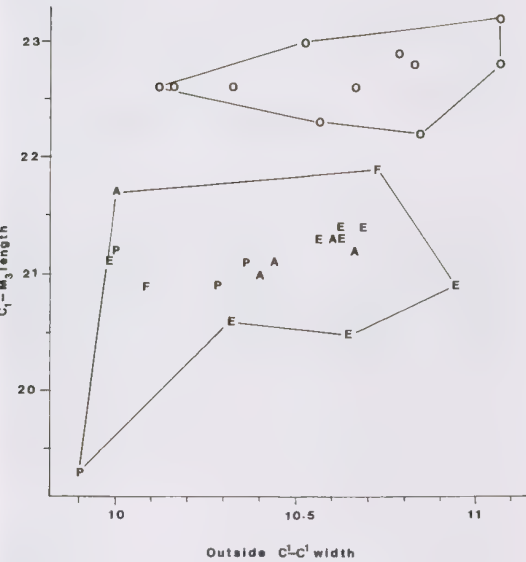


Figure 4 Plot of upper maxillary tooth row length versus width outside C¹C¹.

Table 3 Canonical variate function coefficients from DFA between three groups of *P. lombocensis* (Lombok, Alor, and Flores-Lembata-Pantar) based on five characters (see text). Standardised values, followed by (in brackets) unstandardised values.

CHARACTER	FUNCTION 1	FUNCTION 2
C ₁ M ₃	0.8254 (1.7860)	-0.1482 (-0.3207)
M'B	0.4364 (4.0404)	-0.6423 (-5.9471)
C'M ²	0.2916 (0.8321)	1.0210 (2.9131)
RL	-0.4357 (-0.7906)	-0.9400 (-1.7058)
D4M	-0.1074 (-0.0393)	0.7278 (0.2661)
CONSTANT	-51.1681	-30.9264
Variance explained (%)	87.9	12.1

Diagnosis

Averages larger than *Pteropus lombocensis heudei* for all characters except mesopterygoid fossa breadth, digit 3 phalanx 2 length and ear length (see Table 1). C₁M₃ is larger relative to width outside C'C' (Figure 4). The colour of the collar at the neck, base of head, throat and upper chest is a darker Cinnamon – Cinnamon Rufous compared to Cream Color to Buff Yellow.

Description

See Andersen (1912: 266–9) for a detailed description of pelage, skull, dentary, teeth and palatal ridges.

Distribution

Lombok and Sumbawa Islands.

Remarks

The juvenile and subadult specimens from Sumbawa Island have pelage colour and teeth dimensions similar to the adult specimens from Lombok Island. They are referred to *P. l. lombocensis*.

Pteropus lombocensis heudei Matschie, 1899

Pteropus heudei Matschie, 1899: 32.

Pteropus tricolor Heude, 1896: 177, footnote, pl. v. fig. 7 (teeth) (preoccupied).

Pteropus solitarius K. Andersen, 1908: 367.

Holotype

Andersen (1912: 269) states that “type presumably in the Zi-ka-wei Museum, near Shanghai”.

Type locality

Flores Island, Nusa Tenggara.

Specimens examined

Flores Island (all adults)

Desa Ratulodong, 8°11'S, 122°52'E, 1♂ 1♀, WAM M(32563, 32568).

Lembata Island

Desa Belang Watokob, 8°26'S, 123°22'E, 1♂ 5♀, WAM M(32152, 32154, 32178, 32211–2, 32455); Desa Boto, 8°31'S, 123°23'E, 1♂ 1♀, WAM M32453–4.

Pantar Island

Desa Batu Bakalang, 8°14'S, 124°18'E, 4, WAM M37757–60.

Alor Island

Kota Kalabahi, 8°14'S, 124°32'E, 1♂ 3♀, WAM M37637–40; Desa Apui, 8°15'S, 124°43'E, 1♂, WAM M37996.

Diagnosis

Pteropus lombocensis heudei differs from *P. l. lombocensis* as described in the earlier diagnosis of that subspecies.

Description

See Andersen (1912: 269–71, Fig. 13) for a detailed description of pelage, skull, dentary and teeth (figured for *P. solitarius*) and palatal ridges.

Distribution

Flores, Lembata, Pantar and Alor Islands.

GENERAL DISCUSSION

Pteropus lombocensis is restricted to the volcanic islands of the inner Banda Arc, from Lombok Island in the west to Alor Island in the east. In this region it coexists with both the very large *Pteropus vampyrus* Linnaeus, 1758 (which occurs on Lombok Island and Sumbawa [Hill in Corbet and Hill 1992], Moyo, Flores and Kisar Islands [unpublished records]) and the large *Pteropus alecto alecto* Temminck, 1837 (which occurs on Lombok Island [Hill in Corbet and Hill 1992] and Rinca Island [unpublished records]).

In other parts of Nusa Tenggara, *P. lombocensis* is replaced by the similarly sized, and probably ecologically vicarious, *Pteropus griseus griseus* Geoffroy, 1810 and *Pteropus alecto morio* Andersen,

1908. *Pteropus g. griseus* occurs on Wetar Island (unpublished record), immediately to the east of Alor Island, and some other islands in the gondwanic outer Banda Arc (Timor and Semaui Island [Goodwin 1979] and Roti Island [unpublished record]). A larger form of *P. alecto*, probably *P. alecto gouldi* Peters, 1867, also occurs on Timor Island [unpublished record]. *Pteropus alecto morio* occurs on Sumba and Savu Islands (Hill in Corbet and Hill 1992; unpublished records). *Pteropus vampyrus* occurs on two outer Banda Arc islands, Timor (Goodwin 1979) and Roti (unpublished report).

In conclusion, the small *Pteropus* species in Nusa Tenggara (*P. lombocensis*, *P. g. griseus*, *P. alecto morio*) show a pattern of distribution that is repeated by a number of other bat taxa. That is, a species that is widely distributed in the inner Banda Arc either differentiates morphologically into subspecies in the outer Banda Arc (Sumba, Savu, Roti, Semaui, and Timor) or is replaced there by allied species (see Kitchener *et al.* 1994 a,b)

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of both the current Director, Mr A. Reeves, and the previous Director, Mr J. Bannister, of the Western Australian Museum; Drs M. Amir, Director, Balitbang Zoologi (LIPI); and the Directors of the Department responsible for the conservation of wildlife in Nusa Tenggara Barat, Ir P. Supriadi and Nusa Tenggara Timur, Ir J. Mochtar. To our colleagues Dr R. How and Mr R. Johnstone, Western Australian Museum; Mr A. Gunnell, Curtin University of Technology; and Ir I. Maryanto and Drs A. Suyanto, Museum Zoologicum Bogoriense, who participated in the exhausting field work, we extend our thanks for both their effort and companionship. Dr How kindly reviewed the manuscript.

Expedition costs were defrayed by grants to Dr D. Kitchener from: National Geographic Society, Washington, Australian National Parks and Wildlife Service and the Scott Trust, Sydney. Garuda Indonesia kindly defrayed freight costs of the expeditions. Skulls were prepared by Mr M. Salotti, Western Australian Museum and Mr Wayne Walters, Curtin University of Technology,

the latter also recorded all external measurements. Mrs N. Cooper assisted with the statistical analyses. Mrs A. Nevin, Western Australian Museum kindly typed the manuscript.

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Manuscript received 10 January 1994; accepted 14 July 1994.

Body dimensions in *Simoselaps* and *Vermicella* (Elapidae): a method for determining sex in natural populations

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Abstract – A total of 736 museum specimens of 11 different species of *Simoselaps* and *Vermicella* were examined in the laboratory. Snout–vent lengths and tail–vent lengths were measured and each specimen was sexed by dissection. Within species, females had larger snout–vent lengths than males, but for tail–vent lengths the converse was the case. The tail–body ratio for each specimen was determined by dividing the tail–vent length by the snout–vent length. Males and females of each species had a range of tail–body ratios which did not overlap. Tail–body ratios provide a simple and accurate method for sexing live fossorial snakes.

INTRODUCTION

Small fossorial snakes are among the most abundant snakes in parts of Australia but they are difficult to sample and have therefore attracted little study (Shine 1984). Fifteen species of small fossorial snake are found in Australia and eleven of these occur in Western Australia: *Simoselaps anomalus*, *S. approximans*, *S. bertholdi*, *S. bimaculatus*, *S. calonotos*, *S. fasciolatus*, *S. littoralis*, *S. minimus*, *S. roperi*, *S. semifasciatus* and *Vermicella multifasciata*. Four of them, *S. approximans*, *S. calonotos*, *S. littoralis* and *S. minimus*, are endemic to Western Australia (Storr *et al.* 1986).

The nomenclature used for these fossorial snakes varies among researchers. Some recognise three separate genera within the group (*Neelaps*, *Simoselaps* and *Vermicella*). However, in this paper the generic nomenclature of Cogger (1992) has been followed, with all the burrowing snakes in Western Australia being placed in the genera *Simoselaps* and *Vermicella*. Details of the geographical location and range of each species are described in various texts (Storr 1967; Storr *et al.* 1986; Cogger 1992).

Storr (1967), in his major revision of the burrowing snakes of Western Australia, provided data on the significance of body and tail dimensions in the group and pointed out the "...considerable correlation between the number of ventrals, total length and (inversely) relative length of tail."

The aim of this study is to use museum specimens of fossorial snakes to relate sex to external body dimensions in an attempt extend the work of Storr (1967, 1979) and provide a method of sexing snakes with reasonable confidence in the field.

MATERIALS AND METHODS

Eleven species and 736 specimens of fossorial snake occurring in Western Australia were examined in this study. All specimens are held at the Western Australian Museum. For each specimen the snout–vent length (SVL) and the tail–vent length (TVL) were measured to the nearest millimetre. Sex was determined by dissection and examination of the gonads. In the case of juveniles, or where the internal organs were missing or damaged, the specimens were recorded as unsexed. In a few cases sex was determined for specimens with fractured bodies or broken tails that were not used in further analysis. For *S. bertholdi* and *S. semifasciatus*, both numerically abundant in the collection, only a sample of the available specimens was examined and measured.

The tail–body ratio (TBR) was calculated by dividing the tail–vent length (TVL) by the snout–vent length (SVL) for each specimen.

In the case of two species, *S. fasciolatus* and *V. multifasciata*, specimens from each of the subspecies found in two distinct geographical locations were examined to determine if there was a difference between the geographical populations in the TBRs. *Simoselaps bertholdi* is found throughout a large area of southern and central Western Australia and specimens from different geographical regions within its range were examined to see if the TBR between sexes varied with geographical region. These regions were the southwest of the State, the Pilbara-Gascoyne area in the northwest and the deserts in the east.

The dimorphism in body dimensions between sexes in these fossorial snakes was evaluated by analysis of variance using the Statistix (1992) package.

RESULTS

The mean SVL of females exceeds that of males for all species except *S. anomalus*. The mean TVL is greater in males than females of each species (Table 1).

Tail-body ratio is strongly dimorphic with TBRs of males being higher than females (Table 2) and no overlap occurring between males and females in most species. An exception is observed in *S. fasciolatus fasciolatus* where the minimum male TBR is 0.1186 and the maximum female TBR is 0.1233. However, all other females in this species have a TBR <0.0918. Table 2 also shows the mean and range of tail-body ratios recorded for males and females in the subspecies of *S. fasciolatus* and *V. multifasciata*. The TBRs for the different sexes in the two subspecies *V. multifasciata multifasciata* and *V. multifasciata snelli* are different, with the ranges for the sexes in the two subspecies overlapping. There were insufficient specimens of *S. fasciolatus fasciatus* to allow comparison with the nominate subspecies *S. fasciolatus fasciolatus*.

The juvenile and unsexed *Simoselaps* and

Vermicella specimens in this study were assigned to males and females on the basis of their tail-body ratios and the sex ratio obtained was similar to that of the sexed population.

There is no overlap in TBRs between males and females in *S. bertholdi* from different geographical regions, although there is some variation in the mean TBRs for the two sexes in the different regions. The TBR of southwest males is significantly lower on average than those in the northwest (Mann-Whitney U, $p = 0.0035$) and east ($p = 0.0012$), while females are not significantly different between areas.

DISCUSSION

In snakes it is common for females to exceed males in average size (Fitch, 1981; King 1989). The fossorial snakes investigated in this study follow this trend with females having greater mean SVLs than males and results are similar to those obtained by Shine (1984) in his study of fossorial snakes in Australia. However, *S. anomalus* provides an

Table 1 The mean snout-vent lengths and tail-vent lengths for male and female *Simoselaps* and *Vermicella* together with standard deviation, range and sample size. Significant differences between the sexes at $P < 0.01$ are indicated by a single asterisk (*) and at $P < 0.001$ by a double asterisk (**).

Species	Total	Sex	No	Snout-vent length (cm)			No	Tail-vent length (cm)		
				Mean	SD	Range		Mean	SD	Range
<i>S. anomalus</i>	27	M	18	15.2	1.6	11.5–17.7	18	2.2**	.3	1.6–2.5
		F	5	14.1	3.3	10.5–19.1	5	1.5**	.3	1.1–1.9
<i>S. approximans</i>	31	M	14	27.0	3.4	21.0–32.5	14	2.8**	.4	2.2–3.4
		F	10	27.8	4.1	20.5–35.5	10	2.2**	.2	1.8–2.6
<i>S. bertholdi</i>	213	M	87	16.9**	2.2	10.0–21.8	86	2.3**	.4	1.3–3.0
		F	80	19.7**	3.7	10.0–29.0	81	1.8**	.4	0.9–3.0
<i>S. bimaculatus</i>	65	M	27	24.9**	3.8	19.0–30.5	27	2.6**	.4	2.0–3.2
		F	29	29.8**	5.6	20.5–39.0	28	2.1**	.3	1.4–2.7
<i>S. calonotos</i>	81	M	37	19.3**	1.9	13.8–22.3	36	3.2**	.4	2.3–4.0
		F	32	21.7**	2.3	15.2–25.2	32	2.8**	.3	2.0–3.3
<i>S. littoralis</i>	84	M	29	16.0**	2.0	11.8–20.5	29	2.3	.3	1.7–2.9
		F	40	20.9**	5.3	12.3–35.8	40	2.1	.6	1.1–3.1
<i>S. minimus</i>	3	M	2	17.6	2.3	16.0–19.2	2	2.4	.4	2.1–2.7
		F	1	20.5		20.5–20.5	1	2.1		2.1–2.1
<i>S. roperi</i>	12	M	9	26.2	3.4	21.8–32.5	9	2.6*	.3	2.1–3.0
		F	2	27.6	3.6	24.9–30.0	2	1.8*	.6	1.4–2.2
<i>S. semifasciatus</i>	154	M	65	23.0**	3.4	13.8–30.0	65	2.6**	.4	1.5–3.7
		F	64	26.0**	4.1	15.0–34.2	63	2.0**	.4	1.0–3.0
<i>S. fasciolatus fasciatus</i>	4	M	2	27.5	0.7	27.0–28.0	2	3.7	.1	3.6–3.7
		F								
<i>S. fasciolatus fasciolatus</i>	40	M	18	25.6	4.9	13.4–31.2	18	3.3**	.6	1.7–3.9
		F	17	27.0	7.1	15.0–35.0	17	2.3**	.8	1.1–3.7
<i>V. multifasciata multifasciata</i>	9	M	2	33.3	5.3	29.5–37.0	2	2.4	.2	2.2–2.5
		F	6	41.5	10.2	24.6–51.3	6	1.9	.5	1.0–2.7
<i>V. multifasciata snelli</i>	13	M	4	34.0	2.9	31.1–38.0	4	1.8	.2	1.6–2.0
		F	8	36.4	9.3	21.2–48.5	8	1.5	.4	0.9–2.0

Table 2 The mean tail-body ratios (TBR) for males and females of *Simoselaps* and *Vermicella* together with standard deviation, range and sample size.

Species	Sex	No	Mean TBR	SD X 10 ⁻³	Range	Mid-Point
<i>S. anomalus</i>	M	18	.1461	7.32	.1317 – .1612	.1241
	F	5	.1048	6.87	.0994 – .1164	
<i>S. approximans</i>	M	14	.1039	6.16	.0945 – .1133	.0945
	F	10	.0814	8.16	.0676 – .0945	
<i>S. bertholdi</i>	M	86	.1341	9.48	.1127 – .1525	.1122
	F	80	.0923	7.96	.0777 – .1116	
<i>S. bimaculatus</i>	M	27	.1031	7.04	.0915 – .1157	.0858
	F	28	.0707	5.06	.0589 – .0800	
<i>S. calonotos</i>	M	36	.1642	9.28	.1428 – .1818	.1397
	F	32	.1269	7.48	.1116 – .1366	
<i>S. littoralis</i>	M	29	.1420	8.50	.1277 – .1586	.1222
	F	40	.1028	8.38	.0865 – .1166	
<i>S. minimus</i>	M	2	.1359	6.63	.1312 – .1406	
	F	1	.1024			
<i>S. roperi</i>	M	9	.0994	6.06	.0861 – .1044	.0814
	F	2	.0647	12.1	.0562 – .0766	
<i>S. semifasciatus</i>	M	64	.1141	8.19	.0971 – .1347	.0929
	F	63	.0772	6.24	.0648 – .0888	
<i>S. fasciolatus fasciatus</i>	M	2	.1328	5.99	.1285 – .1370	
	F					
<i>S. fasciolatus fasciolatus</i>	M	18	.1284	5.79	.1186 – .1400	.1052
	F	17	.0852	12.5	.0611 – .0918 (.1233)	
<i>V. multifasciata multifasciata</i>	M	2	.0710	4.96	.0675 – .0745	.0615
	F	6	.0454	7.98	.0350 – .0555	
<i>V. multifasciata snelli</i>	M	4	.0528	2.08	.0514 – .0558	.0492
	F	8	.0403	4.30	.0328 – .0469	

exception that is probably due to the small sample size of females which contains a relatively high proportion of non-adult individuals. Conversely, the mean TVL was found to be larger in males than females in all species studied, which agrees with the findings of King (1989).

In a number of species the difference between males and females is highly significant for both SVL and TVL (Table 1). This occurs particularly in those species where the data set is relatively large. However, measurements of SVL and TVL do not allow determination of sex in themselves, rather, the two measurements taken as a ratio provide a useful tool for determining sex in these snakes.

The results of the study indicate that each species of *Simoselaps* and *Vermicella* in Western Australia has a tail-body ratio that does not overlap between sexes (Table 1) and adds further support to Storr's (1967) finding. One large female *S. fasciolatus fasciolatus*, with an exceptionally long tail, is responsible for the sole instance where overlap occurs in the male and female tail-body ratio ranges (Table 2).

The degree of confidence in determining the sex of specimens is greatly reduced where the data set is small, e.g., *S. minimus*, and tail-body ratios that fall within this zone of separation may prove

difficult to assign to sex. Consequently, in Table 2 the mid point of the zone of separation for each species is presented as a value above and below which the sex for each individual can be assigned.

Significant variation in tail-body ratios is present between the same sexes of the two subspecies of *Vermicella multifasciata*. However, in the study there were insufficient specimens of *S. fasciolatus fasciatus* to make a useful comparison of the TBRs with the subspecies *S. fasciolatus fasciolatus*.

Storr (1967) found the absolute size of *S. bertholdi* specimens increases from the southwest to the north and east and that the relative length of their tails similarly increases. No overlap is found in the male and female TBRs of *S. bertholdi* from three different geographical regions even though the mean TBRs for male specimens from the southwest are significantly lower than the other two regions.

CONCLUSION

The greater Perth Metropolitan region of Western Australia has a rich and abundant reptile fauna comprising over 70 species. Since European settlement this fauna has been modified by development in the form of agriculture and urbanisation with the result that most species now

Table 3 The mean snout-vent length, tail-vent length and tail-body ratio including the standard deviation and range for males and females of *Simoselaps bertholdi* from three different geographical locations within Western Australia.

<i>S. bertholdi</i>		Snout-vent length (cm)				Tail-vent length (cm)				Tail-body ratio				
Geographical location in W.A.	Sex	No	Mean	SD	Range	No	Mean	SD	Range	No	Mean	SD X	Range	10 ⁻³
Southwest	M	56	16.4	2.0	10.0 – 19.5	55	2.2	.3	1.3 – 2.7	55	.1311	9.15	.1127 – .1515	
	F	51	19.0	3.2	10.0 – 25.8	52	1.7	.3	0.9 – 2.3	51	.0909	6.58	.0794 – .1029	
Northwest	M	14	17.3	2.1	12.2 – 20.3	14	2.4	.3	1.7 – 2.8	14	.1397	8.55	.1280 – .1524	
	F	15	19.5	3.7	14.2 – 26.2	15	1.9	.4	1.4 – 2.4	15	.0949	8.61	.0777 – .1116	
East	M	17	18.5	1.9	14.7 – 21.8	17	2.6	.3	1.9 – 3.0	17	.1391	7.06	.1279 – .1525	
	F	14	22.5	4.1	16.3 – 29.0	14	2.1	.4	1.5 – 3.0	14	.0948	6.11	.0827 – .1060	

persist in populations that are isolated on fragments of natural vegetation (How and Dell 1994). Particularly numerous in the near-coastal dune systems are fossorial skinks, legless lizards and snakes (How and Dell 1993). Our study of vertebrate fauna on remnant bushlands in the Perth region has verified that fossorial snakes can be locally abundant and may persist in remnant bushlands for many decades after isolation. Over 270 individuals of five species have been measured and released, with five species sympatric in some habitats. The method of sex determination described in this paper will help in future studies of population dynamics and should also be a useful tool for other field biologists working with these species.

ACKNOWLEDGEMENTS

We would like to thank Ken Aplin for the use of the collections in the Western Australian Museum, and Ken Aplin, Laurie Smith and John Dell for their assistance during this study. Ken Aplin, John Coventry, Rick Shine and John Dell provided valuable comments on an early draft of this paper.

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Manuscript received 26 April 1994; accepted 14 July 1994.

Military firearms in colonial Western Australia: their issue and marking

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Abstract – The types, quantities and dates of issue of military firearms to the Imperial garrison, the Enrolled Pensioner Force, the Volunteer Force, the Permanent Force and the Cadet Force between 1829 – 1903 are examined and discussed. The markings of these arms, where known, are described and discussed. The types, quantities and marking of Western Australian military arms in the early Commonwealth period are also briefly canvassed.

INTRODUCTION

The types, quantities and dates of issue of military arms in Colonial Western Australia have been of interest to arms researchers for many years. Little was known until the pioneering work *The Volunteer Movement in Western Australia 1861 – 1903* was written by George Wieck in the 1960s. Wieck's chronology on the formation and disbandment of the various volunteer corps between 1861 and 1903 has been the standard reference on the subject. His work has since been expanded upon by later writers, notably James Grant, but like Wieck, the focus has remained on personnel, arms being relegated to an incidental status. Broomhall in his valuable reference *The Veterans* includes more information on the Enrolled Pensioners arms, but again the focus is on the men, arms being secondary.

This paper follows the Wieck chronology. The author has checked references to arms given in these and other works and has included additional archival material discovered at this time and during earlier research on *The Martini-Enfield Rifle in Western Australia*. The aim has been to present a chronological description of the arms issued to the Western Australian military. Some discrepancies have arisen regarding the types of arms and their dates of issue as stated in the Wieck reference compared with data presented in this research. Wieck gives 1883 as the date of issue of the Snider-Enfield rifle in Western Australia. This researcher found no reference to this date in the archives, instead 1870 was found to be unequivocally the date of issue of the Snider-Enfields to the Pensioners and 1877 the date of issue of the Sniders to the Volunteers. Chris Halls, in his book *Guns in Australia* quotes the types of arms on issue here, notably the Snider-Enfield two band Artillery Carbine (1880s), and the Martini-Enfield Artillery Carbine (1898) for the Naval Artillery Volunteers. He also writes that the Martini-Enfield Artillery Carbine Mark I was issued in 1900 to the Fremantle

Artillery Volunteers. Again, no archival record on the issue of these arms was found. It is however entirely possible that archival sources were found by these writers, but as the sources were not given they could not be referred to at this time. Similarly, some records of arms issues located for this paper are not referred to by previous writers. It is possible that arms of the types mentioned were indeed issued on the dates stated by Wieck and others and due reference is made to them, but until they can be verified they are included for comparison and comment only. Some volunteer corps such as the Sussex and Swan Volunteer Rifles described in Grant are omitted here due to their never becoming properly active. The various mounted detachments of the volunteer corps which became the W.A. Mounted Infantry in 1900 are also omitted due to the lack of records concerning them. Because the local W.A.M.I. and the Boer War W.A.M.I. detachments used identical arms they are treated as one entity. It was also intended to give a complete account of the marking of volunteer arms but, as will be seen from the text certain sections of the arms marking procedure remain uncertain, notably, some of the Martini-Henrys of the rifle corps and the arms of some of the mounted and artillery corps. What has been presented however greatly clarifies this subject.

Note: Abbreviations which may be found in the text: E.P.F. = Enrolled Pensioner Force, W.A.I.B. = W.A. Infantry Brigade, S.M.L.E. = Short Magazine Lee-Enfield, M L-E = Magazine Lee-Enfield, M.M. = Martini-Metford, M-E = Martini-Enfield, Mk = Mark, B.L. = Breech loading, M.L. = Muzzle loading. The initials of the various corps are used frequently in the text but always in context with the corps under immediate discussion and thus will cause no confusion.

Note also that with the exception of the Deane, Adams revolver-carbine and the W.A. Pattern Martini-Enfields, only the issue and ownership marks of the various firearms under discussion are

illustrated. For full technical details and full length illustrations of these other arms, refer to Skennerton's *Australian Service Longarms*. In some cases it has not been possible to photograph markings, but generally, the markings which are not illustrated are similar in style and marking method to those shown. One last point must be clarified. It will be noticed that Pinjarra is also referred to as Pinjarrah, this is because the old spelling included the "H".

THE IMPERIAL FORCES

Beginning with the first white settlement of Western Australia in 1826, Imperial troops were stationed here until they were withdrawn in 1863. Their arms would have included British service "Brown Bess" flintlock muskets and the various types deriving from it. They were the India Pattern, the New Land Pattern and the Patterns 1839 and 1842 muskets. The 63rd Regiment, arriving here in 1829 included in its stores the following arms which were in addition to their issue "Brown Bess" muskets.

Rifles MFG CB with steel rammers and bayonets	- 20
Carbines, Elliots, with steel rammers	- 20
Muskets, extra service, with rammers and bayonets	- 40
Scabbards, bayonets, muskets	- 60

These arms were to be placed at the disposal of the commanding officer of the West Coast.¹ "Extra service" arms were cheap low quality muskets and bayonets made by the trade. "Elliots carbines" refers to the General Elliot Light dragoon carbine of 1773.² These arms were unlikely to have been marked. Later regiments had the Baker rifle and later still the Pattern 1851, 1853, 1858 and 1860 Enfield long and short rifles.³ Small numbers of most of these types of arms exist in public and private collections but they are generally unmarked except for the Board of Ordnance "B broad arrow O" mark on the butt and are therefore not readily identifiable as Imperial garrison issue arms. The absence of issue markings need not disqualify them as garrison issue arms however as it appears to have been not unusual for them to be unmarked. Skennerton states that "the regular British issue rifles and carbines were not always stamped with the unit markings".⁴ Some of these arms do have the markings of British military units but none so far have been identified as units stationed here. These arms may be surplus regular army or yeomanry weapons sent to W.A. as stores without first having their markings cancelled. It is considered highly likely that most of the arms on issue to Imperial troops probably left with them

when they departed W.A. and those arms which were left here and which have been noted as marked and unmarked, were probably "extra service" and obsolescent arms intended as reserves for the possible defence of the colony. A considerable number of socket bayonets which fit these muskets have been examined and were found to bear no ownership marks or stand numbers whatsoever. This evidence, tenuous though it appears, leads to the conclusion that virtually none of the service arms of the Imperial troops remain here, the surviving arms being the latter miscellaneous types.

THE PENSIONERS

The most significant Imperial force stationed in Western Australia was the Enrolled Pensioner Force, which manned the Convict Establishment in Western Australia. In response to a shortage of labour, convict transportation began in the free colony of Western Australia in 1850 with the arrival of a group of convicts and their Pensioner guards on the *Scindian*. These guards, like the Imperial garrison troops, were funded from Britain, but they were volunteers and are more closely linked to the settlement of the colony than the garrison troops. Many came with their families and remained as settlers. Their official association with W.A. lasted 30 years, with a further seven as the Enrolled Guard.

The Enrolled Pensioner Force came to Western Australia as guards detachments with each lot of convicts arriving between 1850 and 1868. They served from 1850, but the need for this force declined after convict transportation ceased in 1868, leading to reductions of their numbers and final disbandment in 1880. The need to continue to have an armed policing force in the colony was recognised however and a small number of Pensioners were selected to serve on a new force entitled the Enrolled Guard. This group continued the duties of the old force but was more of a gendarmerie. It existed from 1880 to 1887.

Between 1850 and 1868 a total of 1191 guards arrived in the colony. In the early days they were armed with "smoothbore muskets and bayonets"⁵ for the rank and file. The early arms of the Pensioners were probably Pattern 1839 and/or Pattern 1842 muskets. One Enrolled Pensioner Force Pattern 1839 smoothbore musket is known in a private collection, complete with its accoutrements, but is unmarked except for the "B broad arrow O" mark of the Board of Ordnance. Based on such a small sample however it would be premature to conclude that all early E.P.F. arms were unmarked. On one occasion in 1855 the Pensioners apparently applied to England to

upgrade their arms to the new "Minie Rifle", (the Pattern 1851), but instead received "500 or 600 percussion smoothbore muskets". These arms were accompanied by the comment "No Minie rifles are available and it will be some time before they can be spared".⁶ The large number of muskets sent is surprising considering the low number of men actually under arms in W.A. Of the 352 guards here in 1856, only 157 were required to bear arms, and by 1864 the number of armed guards had risen to only 268,⁷ so the large number of arms sent in 1855–56 probably included arms for store. The reason that no Pattern 1851 Minie Rifles were sent was that virtually all of them were needed for regular troops in the Crimea and also, by 1855 the Pattern 1853 rifled musket was well into production and issue. Two years later, in May 1857 the E.P.F. acquired six double barrelled carbines complete with sword bayonets and 120 rounds of carbine ammunition from the W.A. Police Force. These carbines were for use when shipping convicts up and down the coast in boats, where their long muskets proved cumbersome.⁸ It is presumed that these carbines, if marked, would have had the ownership marks of the Police Force.

The new Pattern 1853 Enfield .577 inch calibre muzzle loading rifles began making their appearance at this time and may have accompanied the later Pensioner groups arriving here. They would have arrived in Western Australia probably beginning in the late 1850's or early 1860's but there is also strong evidence suggesting that they were sent as a single large shipment. A reasonable number of Pattern 1853 Enfields survive bearing the engraved marks of the Enrolled Pensioner Force. The mark on the brass buttplate tang is "W.A. over E.F. over number" (see Figure 1). The highest number observed on an Enfield is 260 (W. A. Museum, W73.104). E.P.F. Enfields noted have included Second and Third models of both British and Belgian manufacture. From the similarity of the engraving style of the letters and numbers observed on these Enfields it is concluded that they may have been engraved at the same time by the same hand. Whether they were engraved in England prior to shipment or engraved here at the convict establishment is unknown, but in light of evidence discovered concerning the engraving of volunteer arms, it could well have been done here. From butt numbers observed and known manning levels it is calculated that they were numbered from one to about 300. When these arms were issued they replaced the smoothbore muskets on issue in the metropolitan area but the remote country stations retained their smoothbore muskets for another twenty years. Pattern 1853 Enfield bayonets noted have been marked with stand numbers only, having no additional identifying letter code. The



Figure 1 The engraved ownership marks of the Enrolled Pensioner Force, 1850 – 1880. This mark appears on the butt plate tang of a Pattern 1853 Enfield rifle used by them between c.1860 – 1870. (Photo D. Elford).

stand number range observed indicates that these bayonets are almost certainly W.A.E.F. bayonets. The highest number observed was 267.

The next arm used by the E.P.F. was the Snider-Enfield conversion to breech-loader. According to a despatch included in the 1876 Votes and Proceedings of W.A. Parliament, the E.P.F. received their Snider-Enfields "early in 1870".⁹ The Snider-Enfield .577 inch calibre breech loading rifles were introduced into British service commencing in 1866,¹⁰ and were produced in both the short rifle version for sergeants and the long rifle for rank and file. All E.P.F. Enfield-Sniders noted have been the Mark II** long rifles. These arms were also marked on the brass buttplate tang

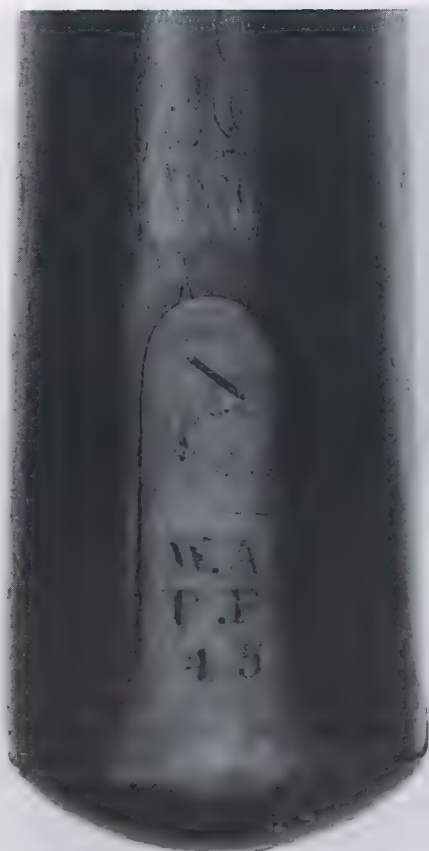


Figure 2 The ownership marks of the Enrolled Pensioner Force. These marks are on the butt plate tang of a Snider-Enfield Mk II** used by them between 1870 – 1880. (Photo D. Elford).

“W.A. over E.F. over number” (See Figure 2). They were engraved in their own series beginning again at one, with the highest number noted being 194. Again, stand numbers observed and manning levels indicate that about 250 were received.¹¹ These more modern arms were also issued where the need was greatest (i.e., Fremantle and Perth), replacing the Enfields which were then loaned to the volunteers.¹² The obsolete smoothbore muskets of the Albany, York, Northam, Greenough and other outstations were never replaced by breech-loaders. It was only the reduction of the Force in 1878 that caused these outstation arms to be recalled, and after total disbandment of the E.P.F. in 1880, they were sold, on January 3rd 1881.¹³

The successor to the Enrolled Pensioner Force was designated the Enrolled Guard and mustered 50 pensioners. The new force received E.P.F. Snider-Enfields with their marks unaltered, the remainder being loaned to the volunteers, also with

their marks intact. It is thought that, being Imperial arms on loan, these marks could not be altered by the colonial government. The Enrolled Force existed until 1887. During the years 1874 – 1887, the E.P.F. and later the Enrolled Guard never took the opportunity to modernise their arms by adopting any of the newer types such as the Martini-Henry.¹⁴

THE VOLUNTEERS

The earliest volunteers were the Swan River Volunteers of 1829 and possibly the Gentlemen Volunteers of 1830. These groups were armed with weapons of types unknown, but may have included those arms listed in the stores of the 63rd Regiment. As the colony was under the protection of Imperial troops their role was actually redundant and was therefore short lived, lasting only until about 1830 or 1831.

The Western Australian Volunteer Force proper began in 1861 and was a response to the announcement that Imperial troops would be withdrawn from garrison in Western Australia by 1863. The first two corps were raised simultaneously, being the **Metropolitan Volunteer Rifles** and the **Fremantle Volunteer Rifles**. The Metropolitan Volunteer Rifles, (also referred to in the records as the Perth Company and the Perth Rifles), consisted of 100 men who were issued initially with “Colonial muskets and accoutrements” borrowed from the Colonial Store.¹⁵ These were probably spare Pattern 1839 or 1842 muskets originally sent to the E.P.F. in 1855. On 13th September 1862 the M.V.R. were issued with “100 new Enfield muzzle-loading percussion rifles recently received as a gift from England”. These Enfields were Pattern 1853 long rifles, the standard British service arm, part of a shipment of “200 Enfield Rifles...received from England per the *Bride* for the use of the Volunteers”.¹⁷ From the very beginning of the volunteer movement the careful recording and issue of arms was undertaken. Barlee, the Colonial Secretary noted on the 9th August 1862:

“The arms shall be marked prior to issue in order to admit of each stand being identified...Places of Arms will have to be fitted up in Perth and Fremantle”.¹⁸

This stand of arms was definitely marked prior to issue as a letter dated August 12, 1862 from the Colonial Secretary to Lt. Col. Bruce, the Commandant of the W.A. Volunteer Force shows. It reads:

“His Excellency the Governor will feel obliged by your making all the necessary arrangements in regard to the marking and issue of the Rifles received per the “*Bride*” for the Volunteers...The Comptroller General (of Convicts) has been requested to send to Perth two convicts who can be employed in marking the arms in such manner as you may direct”.¹⁹

REGULATIONS
FOR THE

Marking and Preservation of Arms issued to
Corps of Colonial Volunteers.

Every Government rifle in the possession of a corps is to bear engraved upon the heel-plate the letter V, and the letter denoting the colony, according to the arrangement given in Appendix A.; the number of the corps should also be added, and the rifles should be numbered consecutively from one upwards, in the manner shown in Appendix B. Care is to be taken that the arms are, in all cases, marked by engraving and not by stamping.

In addition to the letter V no letters except those indicating the colony need be engraved on the rifles issued to rifle volunteer corps; on those issued to light horse, artillery, engineer, and mounted rifle volunteer corps letters denoting the various branches of the service should be added thus—

$\frac{V}{A} \frac{L}{1} \frac{2}{1}$	$\frac{V}{A} \frac{A}{1} \frac{2}{1}$	$\frac{V}{A} \frac{E}{1} \frac{2}{1}$	$\frac{V}{A} \frac{M}{1} \frac{2}{1}$
---------------------------------------	---------------------------------------	---------------------------------------	---------------------------------------

Corresponding letters and numbers are also to be engraved on the socket of the bayonet, on the button of the scabbard, on the rammer immediately under the jag, on the muzzle-stopper, and on the nipple-wrench.

APPENDIX A.

Colony.	Letters denoting Colony.
Antigua	A ^a .
Bahama Islands	B. I.
Barbadoes	B ^a .
Bermuda	B ^a .
British Columbia	B. C.
British Guiana	B. G.
Canada	C ^a .
Cape of Good Hope	C. H.
Dominica	D ^a .
Gambia	G ^a .
Gold Coast	G. C.
Grenada	G ^a .
Heligoland	H ^a .
Honduras	H ^a .
Jamaica	J ^a .
Montserrat	M ^a .
Natal	N ^a .
Norvis	N ^a .
New Brunswick	N. B.
Newfoundland	N ^a .
New South Wales	N. W.
New Zealand	N. Z.
Nova Scotia	N. S.
Prince Edward Island	P. E. I.
Queensland	Q. L.
St. Christopher	S ^a . C.
St. Helena	S ^a . H.
St. Lucia	S ^a . L.
St. Vincent	S ^a . V.
Sierra Leone	S. L.
South Australia	S. A.
Tasmania	T ^a .
Tobago	T ^a .
Trinidad	T ^a .
Turks Islands	T. I.
Vancouver Island	V ^a . I.
Victoria	V ^a .
Virgin Island	V ^a . I.
West Australia	W. A.

Figure 3 Extract from the regulations governing the marking of Volunteer arms. This War Office publication was circulated to all British colonies in 1862 and governed the marking of Imperial arms on issue in the colonies. Colonial owned arms did not necessarily have to conform to these regulations. (Photo V. McNerney).

In 1862 a War Office circular entitled "Regulations for the Marking and Preservation of Arms issued to Corps of Colonial Volunteers" was received in W.A.²⁰ (see Figure 3). It set out the regulation letter and number codes for the marking of volunteer arms such as those sent on the *Bride*.

The regulation mark for a rifle volunteer corps was the letter "V" engraved on the tang of the buttplate followed by the ownership code for the colony and then the stand number of the arm, thus, for Western Australia it was "V over WA over 1". They were to be numbered consecutively from one upwards. The arms were to be engraved, not stamped. The bayonet socket and other small accoutrements were also to be marked. From this regulation it is evident that the individual identity of a particular corps would not be recorded, as the various rifle corps would be issued with arms marked simply "V over W A over number" (see Figures 9 and 10). Only a register of the stand numbers would enable one to identify whether an arm was on issue at Perth or Fremantle. No Pattern 1853 Enfield muzzle loading rifle is known to the author with this "V over W A" marking, but in view of later correspondence from the Commandant of Volunteers it can be stated with reasonable confidence that the letters "V over W A" were used. The Commandant, in an 1864 letter discusses the marking of the next documented shipment of arms (for the Pinjarrah corps), which he desired to have marked to War Office instructions "as in the case of the Enfield Rifles".²¹ This document seems to confirm that the Enfields were marked in the prescribed manner. A possible alternative marking is discussed at the end of the section below, entitled, "Review of Marking".

The Metropolitan Volunteer Rifles were armed with Enfields and lasted ten years until 1872 when they were abruptly disbanded. The arms of this corps were immediately returned to store. One rifle, on issue to Private William Elsegood of the disbanded corps was not returned. This matter was viewed very seriously as the Commandants report of 5th July 1872 to the Commissariat shows:

"W. Elsegood has lost his Volunteer Rifle. Referred to Colonial Secretary in order that he may be pleased to cause steps to be taken for the recovery of the Rifle which can ill be spared. It appears that W. Elsegood belonged to the disbanded company of the Perth Volunteers and as yet has not handed in his Rifle"

The laconic reply from the Colonial Secretary, noted on the margin of this correspondence, was that "W. Elsegood be called upon to return the Rifle".²² It appears that by 29th November 1872 Elsegood's rifle was still missing as there is a reference in this same correspondence to "Enfield Rifle No. 234 lost or mislaid by Volunteer Wm. Elsegood of Perth Company". This man is the only rifle volunteer whose rifle stand number is known.

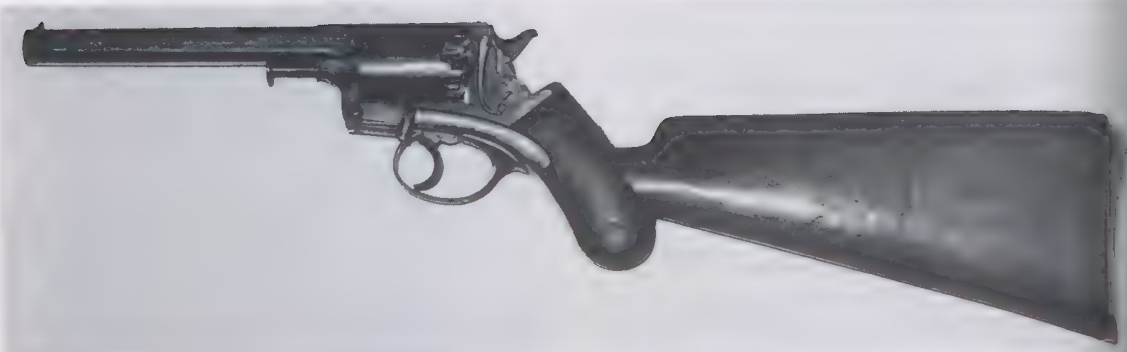


Figure 4 The Deane, Adams and Deane revolver-carbine issued to the Pinjarrah Mounted Volunteers in 1864. (Photo H.49 W.A.M. History Dept.).

As the previous corps' stand numbers are known to reach 100 only, this high number indicates that Private Elsegood's rifle was one of the E.P.F. Enfields on loan.

The Fremantle Volunteer Rifles, raised at the same time as the Perth corps, were also initially issued with "obsolete muzzle-loading muskets".²³ Their arms were also probably Pattern 1839 or 1842 muskets "from the War Office stocks held in the Colony".²⁴ These obsolete muskets were followed in August 1862 with Pattern 1853 Enfields, part of the consignment of 200 sent from England per the *Bride* and also issued to the Metropolitan Volunteer Rifles.²⁵ The Fremantle corps arms were also marked according to the War Office instructions with "V over W A". This corps rose to a peak enrolment of 69 members and was disbanded in 1870.

The next two corps to be raised were mounted volunteers. The **Pinjarrah Mounted Volunteers** were first in 1862, under the command of Captain Fawcett. According to Wieck, the P.M.V. were initially issued with "six revolver-carbines obtained from the guard of a prison ship" followed by 18 "revolver-carbines received in 1864".²⁶ No record of the loan of the prison arms was found but the later revolver-carbines are known to have been commercial Beaumont-Adams revolvers of 38 bore (.50 inch) marketed by Deane, Adams and Deane of Birmingham (see Figure 4). The non-detachable carbine stocks were fitted at the Royal Small Arms Factory at Enfield and they were then sent to Western Australia.

These 18 revolvers were acquired especially for the P.M.V. by the Colonial government. They arrived in October 1864 and were sent immediately by "McLarty's team" down to Pinjarrah without first being inspected and marked. This led to an interesting series of letters from the Commandant and the Colonial Secretary. In a memo from Lt. Col. Bruce dated 5th October 1864 he states:

"I have been verbally informed that the Carbine Revolvers applied for by His Excellency the Governor

for the Pinjarrah Mounted Volunteers have been dispatched to Pinjarrah.

They ought to have been inspected and reported on by a Board after landing.

They should have been marked before issue arguably to War Office instructions as in the case of the Enfield Rifles. I recommend that steps be taken to engrave numbers from 1 to 18 on the several carbines with the initials W.A.V., for instance W.A.V. No. 1, W.A.V. No. 2 etc.

The engraving should be executed on the barrel, on the shifting breach (sic) chamber and on the stock, so as to guard against any of the component parts being changed."²⁷

In the event, these instructions were **not** properly carried out. The Prison provided a convict engraver, "Reg. 7520, C. Reichberg",²⁸ to do the work, but the specimens examined are actually marked "W.A.P.M.V. No." on the top of the barrel only (see Figure 5). It was evidently felt that as the butts of these arms were not detachable there was no danger of them "being changed", consequently none of them were marked with stand numbers (see Figure 6).

It can be seen from the regulations already referred to that the Commandant was slightly in error in his instruction to mark the arms "W.A.V. No. 1", as in fact "V over W A" was stipulated. The War Office regulations also stipulated that in the case of corps other than rifle (infantry)



Figure 5 The ownership marks of the W.A. Pinjarrah Mounted Volunteers, 1864 – 1882. This mark was engraved by a convict in 1864. (Photo Mackaay).

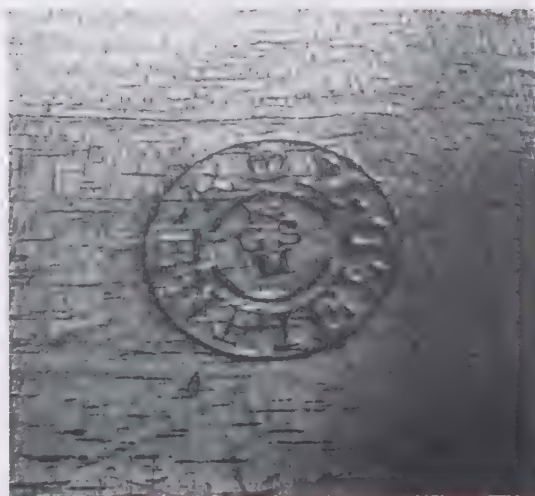


Figure 6 The roundel stamped on the butt of the Deane, Adams revolver-carbine by the Enfield manufactory. Enfield was responsible for the supply of the butts of these arms. (Photo H.49 W.A.M. History Dept.).

volunteers, such as light horse, artillery, engineers and mounted rifles, their arms were to be marked to show the particular branch of the force to which they were issued. Thus, "V over W A A over number" would be the code for the artillery. "V over W A M over number" would be the code for the mounted rifles and "V over W A E over number" the code for the Engineers etc. etc. It can be seen therefore that although not in the prescribed order, the initials "W.A.P.M.V." reflects the branch of the force the arms were issued to more accurately than the "W.A.V." requested by Lt. Col. Bruce. This instance of the marking of an individual corps identity is one of the few known cases of it occurring. "W.A.P.M.V. No." is at odds with the strict regulation guidelines and contrary to Bruce's instructions but it is reasonable to assume that Captain Fawcett's strong personality, the isolation of Pinjarra in those days and the timidity of a probationary convict all combined to produce this decidedly individual marking.

It appears that these revolver-carbines were not very satisfactory, being large and clumsy for cavalry. Capt. Fawcett began to request replacement arms as early as 1868. In a letter dated 21st October 1875, the new Commandant, Lt. Col. Harvest wrote to the Colonial Secretary concerning the P.M.V. He stated that they performed creditably but that they had always suffered from a deficiency "in every article – arms, uniform and equipment", and reported that the men had lately been issued with 12 swords and some bridles. He included a recommendation for the placing of an order for "20 pistols, 5 double rein bridles and 30

pair riding boots" and enclosed a copy of a letter from Captain Fawcett, the P.M.V.'s commander, stating the corps position regarding arms.²⁹ The letter stated:

"Our present Revolver-carbines were part of the armament of the convict ship *Hugomont* (sic) and are only serviceable for marines. They were issued in 1865 and I reported to Colonel Bruce they were unsuitable for cavalry (2nd November 1868)."³⁰

Although Wieck states (p.30) that the P.M.V. never received any other arms, it is evident from the following correspondence that this is not the case. Lt. Col. Harvest wrote again to the Colonial Secretary on 26th November 1875:

"The Pinjarrah Mounted Volunteers have at present cumbersome useless pistols (that is, useless for mounted infantry) and should be provided with a few light revolving pistols".³¹

Subsequent correspondence shows that this request was eventually addressed. On 15th February 1876 Lt. Col. Harvest, Inspector of Volunteers wrote to the Colonial Secretary requesting permission to order "Twenty small Smith & Wesson No. 2 revolver pistols".³² A Crown Agent (London) letter in reply to the Colonial Secretary's order for these arms dated 18th July 1876 states:

"...the pistols cannot be supplied not being of service pattern. The Crown Agents have already ordered from Messrs Blakemore 20 S & W No. 2 Revolvers & Rods & 3500 Cartridges at a cost of fifty one pounds thirteen shillings".³³

These revolvers are identified as either Smith & Wesson .32 inch calibre rimfire, Number 2 Army revolvers, manufactured in the United States between 1861 – 1874 or Smith & Wesson .38 inch calibre centre fire, Model 2 (Baby Russian) revolvers manufactured between 1876 – 1877³⁴ (see Figures 7 and 8).

On 17th February 1877 Lt. Col. Harvest sent a receipt to the Colonial Secretary's Office, it reads "Received from Ernest Howard esq. Colonial Secretary's Office, the undermentioned for the use of the Pinjarrah Mounted Volunteers. 20 Pistols".³⁵ On the same day Harvest wrote to Howard enquiring about the ammunition:

"Where is the ammunition for the pistols you have sent me? The letter from the Crown Agents dated 18th July 1876 mentioned '20 revolvers and 3500 cartridges.' I have telegraphed to Capt. Fawcett to call at my office for the pistols when he comes to town and I should like to be able to give him the ammunition at the same time. It can be deposited in the magazine at the Perth Barracks."³⁶

This letter is definite proof that the P.M.V. received additional arms after the Deane, Adams revolvers, and they appear in the W.A. Returns between 1880 – 1882 which record this unit as being armed with "Light Cavalry Swords and Revolvers". As the number of men rose to 29 in the 1880 Returns,³⁷ these additional men must have

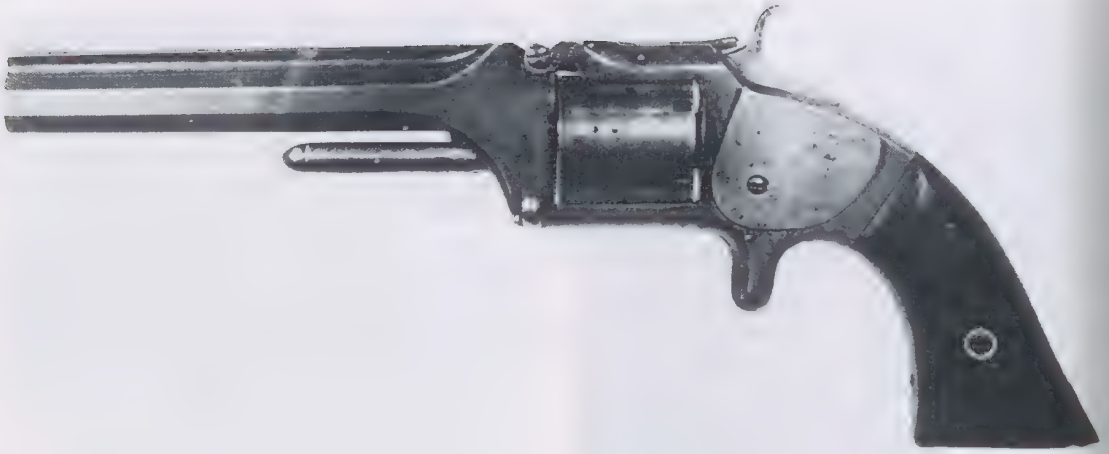


Figure 7 The Smith & Wesson No 2 Army revolver, calibre .32 rimfire.

also been armed, probably with a mixture of Deane, Adams revolver-carbines and Smith & Wesson revolvers. From its earliest days there has always been something of a question mark concerning the arms used by the P.M.V. A Return for 1870 states that 26 men were present for muster, but 40 men "could not parade for want of equipment and uniform".³⁸ Hall states that he thinks these men were armed with 1840 Constabulary carbines, Pattern 1844 Yeomanry carbines and Pagets carbines converted to the percussion system,³⁹ but as yet no evidence of such issues has been found. Numbers of these types of arms exist in collections but none are marked to the P.M.V. except the Deane, Adams revolver-

carbines. The Western Australian Museum holds two of these revolver-carbines, numbers four and five (W72.37 and W743 (see Figure 6). Number five belonged to Captain Fawcett. There is no mention in the archives regarding the marking of the Smith & Wesson pistols of 1877. This corps was disbanded in 1882. There is a record in the Colonial Secretary's Subject Register that Lt. Col. Angelo, the then Commandant, disposed of the P.M.V. arms on 28th August 1883.⁴⁰ A light cavalry sword with its blade etched "Pinjarrah Mounted Volunteers" is known in a private collection.

The second mounted corps, the Union Troop of Western Australian Mounted Volunteers consisted of 33 men and lasted only from 1870 until 1872.

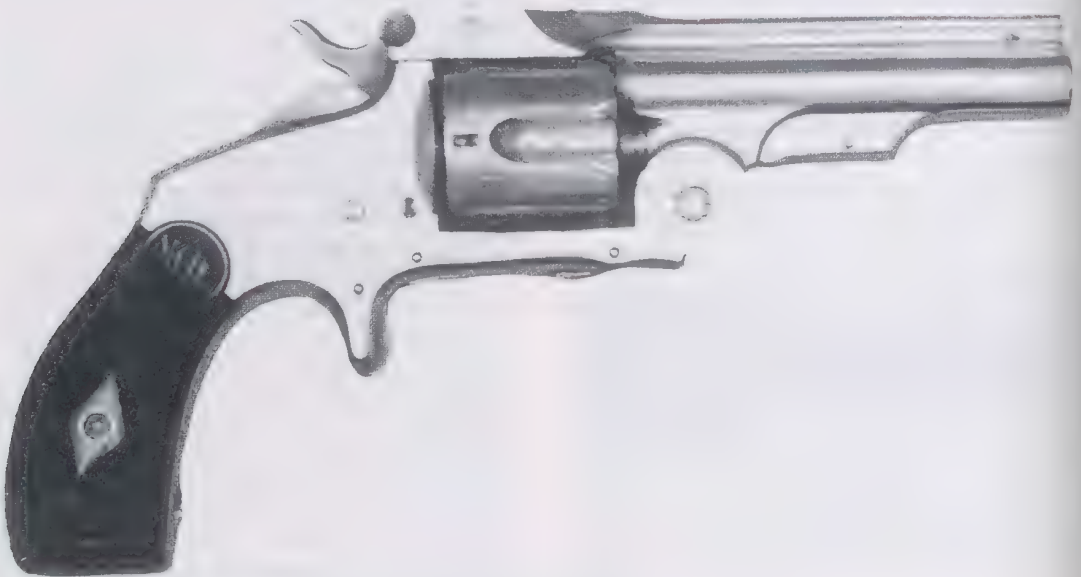


Figure 8 The Smith & Wesson No 2 revolver, calibre .38 centrefire.

their arms being unknown. In 1872 this troop became known as the **Western Australian Troop of Volunteer Horse Artillery**. Their small arms are not known with certainty but W.A. is known to have attempted to procure 30 Martini-Henry .577/.450 inch calibre carbines for them in 1872.⁴¹ In 1874 it is recorded that two copies of a book on "Artillery Carbine Exercises" were received. As the W.A.T.V.H.A. were the only artillery corps at the time it indicates the possibility that they may have been armed with artillery carbines.⁴² The following information however seems to indicate that this corps had no firearms on issue. Photographs of them taken in 1875 and 1879 show them armed only with swords,⁴³ and an 1874 confidential despatch from the Governor to England states that the V.H.A. "has the use of Snider Rifles"⁴⁴ indicating that the troop borrowed arms when required. Also, when the stores of the disbanded Enrolled Pensioner Force were transferred to the W.A. government in 1880, a voucher to the Colonial Storekeeper, J. Flynn, for ammunition used since 1878 was included. The voucher was for "6000 Rounds, Snider Ball for Captain Phillips of the Volunteer Horse Artillery",⁴⁵ It is certain therefore that the troop had access to Sniders (for target practice) at least from 1874 – 1880. Prior to 1877 the "Sniders" could only be the .577 inch Snider-Enfield rifles of the E.P.F. who at that time had the only Sniders in W.A. After 1877 Sniders were on issue to the volunteers but all are thought to have gone to the rifle corps. This corps was again re-named in 1882 as the Perth Artillery Volunteers, with a muster of 25 men and 7 recruits.⁴⁶ They are listed in a Stores Return for 1884 as having "light and heavy swords, 12 Revolvers, 5 Revolving Carbines and 4 Rifles, Enfields". The carbines and Enfields were listed as "unserviceable".⁴⁷ It is difficult to interpret these arms other than to say that there appears still to have been no official "stand" of arms, rather, an oddment of leftovers. The arms listed as unserviceable were probably so due to a lack of muzzle loading ammunition at that late date. The corps are reported in 1887 however to have been awaiting the arrival of a shipment of Martini-Henrys "expected soon".⁴⁸ If they received the Martinis they would have been the first recognizable stand of arms the corps is known to have possessed. This unit became the Number 1 (Perth) Battery, Field Artillery in 1897. They bore this name through until 1903. The arms issued in this latter period and details of their marking are unknown.

In the initial period of the Volunteer Movement 1861 to 1872, only four corps were formed and by 1869 mustered 98 N.C.O.s and men at Perth, 60 at Fremantle and 76 at Pinjarrah.⁴⁹ The last mounted corps, the Union Troop of Western Australian

Mounted Volunteers, already mentioned, was not raised until 1870, when its muster stood at 40 officers and men for a grand total of 272 W.A. volunteers.⁵⁰ By 1872 the two rifle corps had been disbanded, and the 200 Enfield M.L. rifles shared by the Metropolitan and Fremantle Rifle Volunteers were returned to store, leaving only the two mounted corps with less than 100 arms on issue to defend the colony. These totals illustrate the relatively small number of arms existing then, which is not surprising when the entire population, (including convicts) in 1867 was only 21,718.⁵¹

The next period of the Volunteer Movement began in 1872 and went through Federation until 1903. It included a major restructuring in 1893. This period began with the raising of the Perth Company of the Western Australian Rifle Volunteers in 1872, which soon became known as the **Metropolitan Rifle Volunteers**. The M.R.V. included many members of the disbanded Metropolitan Volunteer Rifles. On 14th June 1872 Captain Finnerty the Commandant of Volunteers, recommended to the Colonial Secretary that Captain Birch, the newly designated commanding officer of the M.R.V. be empowered to swear in the volunteers and issue "Enfield Rifles and accoutrements".⁵² The recommendation was accepted and consequently, on 20th June 1872, Finnerty applied to the Colonial Secretary for "100 Enfields for Captain Birch and the new company of volunteers".⁵³ Birch had actually applied to Finnerty to arm the men with breech-loaders (ie. E.P.F. Snider-Enfields) to put them "...on a par with the Pensioners when we are exercising with them"⁵⁴ but this request was not granted. Instead, as has been noted, they were armed with 100 Enfields which appear to have consisted wholly or partly of E.P.F. surplus Enfield arms loaned to the colony.⁵⁵

The M.R.V. was increasing in numbers and according to the Returns of 1874 stood at 122 men.⁵⁶ On the 26th November 1875 Lt. Col. Harvest, the Inspector of Volunteers wrote to the Colonial Secretary stating:

"The Perth Rifle Corps (M.R.V.) should I think be armed with Snider Rifles – their present arms, Enfields on loan from the Imperial Government would then be available to complete the Guildford Volunteers and supply York and Newcastle" and "The Enfields now on loan were spare in the Colony owing to the Pensioner Force being armed with Sniders".⁵⁷

The M.R.V. continued to increase and in that year had a muster of 125 men armed with Enfields.⁵⁸ Soon after, on 18th February 1876, Lt. Col. Harvest ordered new arms consisting of:

"Arms, inter., Rifles B/L Snider with C/R, Short Pat/ 60, Steel Barrels P/III 7.
Rifles B/L inter., Snider with C/R Pat. 53, Steel Barrels, P/III Long Butts 2nd Class 131".⁵⁹

On 17th February 1877 he received per barque *Clifton*, 131 Pattern 1853 Snider .577 inch calibre long rifles and bayonets and seven Snider short rifles with sword bayonets. One chest of 20 long rifles was water damaged and was sold at auction on 11th April 1877, leaving Harvest with 111 long and seven short Sniders which he intended issuing "immediately" to the M.R.V.⁶⁰ Harvest was disappointed as to the quantity of Sniders he could get for his Defence Estimate vote and in September 1876, seven months after the Sniders were ordered, sought to have an additional 24 Sniders purchased from the War Office in London at a reduced rate.⁶¹ He received these latter arms in mid 1877, some months after the original shipment arrived. Instead of the 24 calculated for in the second order, the quantity sent per the *Eulie* was three chests containing "33 Snider-Enfield Rifles, Steel Barrels, Mark III, Short butt, 2nd Class". Harvest wrote in the margin of the shipping advice "24 requested 15 September 1876, 33 sent – so much the better as a case of the previous lot is lost to us".⁶² The M.R.V. were issued some of these 33 rifles in addition to the original 118 long and short Sniders received per the *Clifton*.⁶³

The question of marking the arms arose immediately upon receipt of the *Clifton* lot of Sniders, with Harvest writing to the Colonial Secretary on 17th February 1877.

"Propose to receive rifles for Perth Rifle Volunteers (M.R.V.) as soon as landed from *Clifton*, should be engraved according to regulations before issue to corps. Suggest the engraver be furnished from the Convict Establishment to execute the work in the armoury adjoining the guard in No. 2 Pensioner Barracks at Fremantle".⁶⁴

On the same date Harvest wrote again to the Colonial Secretary's Office seeking advice as to the wishes of the Governor regarding the marking of the arms, whether they should be engraved

"from 1 throughout with 'M.R.V.' Metropolitan Rifle Volunteers, for whom the arms are immediately intended or 'W.A.V.' Western Australian Volunteers...or issued without marks".⁶⁵

The Colonial Secretary's Office commented on 22nd February 1877:

"I also agree with Col. Harvest as to the engraving of the sound rifles in that these be numbered throughout, with the letters 'W.A.V.' which I think would be better than 'M.R.V.' but on this point I am willing to defer to Col. Harvest's opinion if he considers the latter initials preferable. The Engineers can I think be sent to Perth to do the work under Col. Harvest's superintendence".⁶⁶

The location where the engraving was to be done and the personnel to do the work were settled in a letter from Lt. Col. Harvest to Mr. Howard of the Colonial Secretary's Office on 16th March 1877. In response to a delay in the supply of engraving tools made at the Fremantle Prison, Harvest wrote:

"There is some difficulty about certain tools and chisels – required by Prisoner Davis for engraving the Volunteers Arms he is at work on...will you kindly have this matter put right and the tools sent up? This engraving is slow work and we can't afford the delay of sending to Fremantle".⁶⁷

From this correspondence much is again clarified about the engraving of colonial arms, except which letters were eventually decided upon. In view of the reference in Harvest's letter to the engraving of the arms "according to regulations" and his preference for "W.A.V", it is reasonable to conclude that they were indeed engraved that way rather than "M.R.V.". This conclusion is supported by the fact that the latter letters are unknown on any Western Australian Snider arm at this time, while the regulation "V over W A over number" is known on four Western Australian Snider arms. (see Figure 9). These are a Pattern 1860 Snider short rifle Mark III engraved on the wood of the butt "V over W.A. over 5 over P". (W. A. Museum W85.22) and a Snider long rifle Mark III engraved on the brass buttplate tang "V over W A over 50 over P" (W.A. Museum W73.91). The third and fourth rifles, in private collections, are also Snider long rifles Mark III, marked respectively, "V over W A over 77 over P" and "V over W A over 99 over P" on the brass buttplate tangs (see Figure 10). The reason the short rifle is engraved on the wood rather than the buttplate is possibly explained by the fact that the buttplate of the short rifle is case-hardened iron rather than soft brass and may have been too hard for the homemade engraving tools made in the Convict Establishment workshops. The meaning of the letter "P" is unknown but may indicate issue to the Perth company of the W.A. Volunteers or "Purchase", to signify colonially purchased arms rather than Imperial arms on loan. These "V over WA" marks conform to the regulations of 1862, and the Mark (III) of these arms conforms to the 1877 order. It is interesting to note that Snider rifle "V over W A over 99 over P", still has the correct slotted, squared tip cleaning rod present. Although from another rifle, it is from the same 1877 group of 151 Snider Mark IIIs arriving in two batches in that year. The rod is marked across the shaft, just below the tip, "V over 150", indicating that the small accoutrements also were marked according to regulations. Several Pattern 1853 Enfield bayonets have been noted with this marking, such as "V over 16", which is in the W.A. Museum collection (W 1328).

The 1881 Returns show the M.R.V. as being armed with 140 Sniders,⁶⁸ confirming that they were issued most of the additional 33 Sniders received later in 1877. Correspondence confirms that Prisoner Davis, now free, also engraved these second order Sniders.⁶⁹ In a Minute dated 15th January 1884, this corps is listed as having in its



Figure 9 The ownership marks of the W.A. Volunteers, 1862 – c.1882. This mark was engraved on the butt plate tang of Enfield and Snider long rifles. The short rifles of the sergeants, having hard iron butt plates were engraved on the wood instead. The “P” is thought to indicate the Perth company of the Volunteers or “Purchase”, to distinguish these arms as colonial government property, rather than Imperial arms on loan. (Photo D. Elford).

10 ditto for Sergeants.
100 bayonets, common.
10 sword bayonets for Sergeants”.⁷²

The rifles were described as “latest Pattern” (Mk III), “for the Metropolitan Rifle Volunteers”. The M.R.V. are recorded as receiving an additional 30 Martini-Henrys in 1886, taking their total to at least 140 stand.⁷³ The markings of two of the M.R.V. Martini-Henrys are known. One is a Mark II, dated 1880, and is marked, (upside down), on the left side of the butt “M R V over 96”. The stand number, “96”, in large numerals, appears a second time on the opposite (right) side of the butt (see Figures 11 and 12). The second rifle, in poor condition, is an Enfield Mark I dated 1873, converted to become a Mark II. The butt is marked in an identical way to the rifle just described, except that the butt mark is “M R V over 8”.⁷⁴ A number of W.A. issue Pattern 1876 socket bayonets, which originally accompanied these rifles have been examined, and they and some of their scabbards have been noted as being marked with stand numbers, but without identifying letters. All bayonets were numbered, but only a small number of the scabbard studs were. The highest number noted on a bayonet was 118, while the highest



Figure 10 The ownership marks of the W.A. Volunteers. This long Snider Mark III was one of a lot shipped to W.A. in 1877. These arms were engraved by a convict. (Photo Author).

charge in store 130 long Snider rifles and six short Snider rifles. It is noted that “Long rifle number 40 is deficient its bayonet”⁷⁰, indicating again that in accordance with the regulations of 1862, the bayonets were marked to the rifle.

In the Returns to 31st December 1884 this corps is listed as having 120 men armed with Martini-Henry .577/.450 inch rifles.⁷¹ These Martini-Henrys were ordered on 13th August 1883. They were listed as:

“100 Rifles, B.L. with Cleaning Rods, Martini-Henry, long butts for Rank and File.



Figure 11 The ownership marks of the Metropolitan Rifle Volunteers, stamped into the left side of the butt of a Martini-Henry rifle, Mark II. The initials are "M R V over 96". (Photo Author).

scabbard number was 23. Like the Pattern 1853 Enfield and Snider bayonets, the Martini-Henry bayonet is impossible to allocate to a corps unless an arms register is found.

In 1895, as A and B companies of the 1st Infantry Volunteer Regiment, the corps numbered only 65 men who were armed with the new Martini-Metford .303 inch rifles.⁷⁵ The Martini-Metfords issued to this unit were part of 700 Martini-Metford Mark I (W.A. Pattern) rifles which were ordered in 1893 and arrived in July–August 1895 per the *S.S. Nairnshire*.⁷⁶ These arms fixed the Pattern 1888 sword bayonet and were simply marked "W A over number" on the right side of the butt, omitting the prefix "V", the letters and numbers being separated by a thin horizontal line (see Figure

13). The rifle in Figure 13 is from the W.A. Museum Collection (T298).

This corps was absorbed by the Western Australian Infantry Brigade as the 1st Battalion in 1900. They were then issued with 229 of the 1000 Magazine Lee-Speed .303 inch repeating rifles ordered and received in 1900.⁷⁷ The Lee-Speeds also fixed the Pattern 1888 bayonet and were marked on the butt simply "W A over number" (see Figure 14).

The Fremantle Rifle Volunteers were established in 1872 under Captain Sutherland. A letter from Lt. Col. Harvest to the Colonial Secretary on 18th March 1873 states that part of their accoutrements were made in the Convict Establishment at Fremantle.⁷⁸ Again, on the 19th Harvest writes to



Figure 12 The stand number "96", is repeated in large numerals on the right side of the butt of the Metropolitan Rifle Volunteers Martini-Henry Mark II, illustrated in Figure 11. (Photo Author).



Figure 13 The ownership marks of the W.A. Defence Force, 1893 – 1903. The initials “W A” are stamped with individual punches on the right side of the butt of a Martini-Metford Mark I rifle, W.A. Pattern. (Photo D. Elford).

the Colonial Secretary regarding his inspection of the new Fremantle corps which mustered 53 NCOs and men (not counting 19 unavoidably absent from parade). They were imperfectly equipped, being short of about 40 pouches and some belts which could not be made at the Prison due to shortage of material. Regarding arms Harvest wrote:

“They have at present 50 Enfield Rifles and some old smooth-bore muskets I lent them from the Pensioner Store – they ought to be armed with rifles of one uniform pattern – I recommend that 72 Stand of

Martini-Henry long Rifle / steel barrel / complete with Bayonets etc., be procured for them as speedily as possible”.⁷⁹

In a marginal note, Harvest clarifies the “72 Stand” as “68 Long for the Rank and File and 4 Short for Sergeants”, which, since the Martini-Henry did not have a short model, betrays Harvests unfamiliarity with the new arm. He continues with an order for “12,000 ball and 3000 Blank Rds” of ammunition for the Martini-Henrys. Included with this order is a discussion of the



Figure 14 The ownership marks of the W.A. Defence Force, 1900 – 1903. This mark is stamped on the right side of the butt of a Magazine Lee-Speed rifle. Note the mismatched letter punches used. (Photo D. Stein).

differing price structures offered by the British War Office. Apparently stores ordered under "No. 1 Balance Sheet" were a different price from those stores purchased under "No. 2 Balance Sheet", and as Martini-Henry ammunition was about 10 shillings per 1000 more expensive than Snider ammunition, the purchase of it under the most generous balance sheet should be investigated – the new Martini-Henry and Snider rifles costing about the same. Harvest probably sowed the seeds of later confusion over the supply of the Martini-Henry rifles and their ammunition at this time, as he concluded his order to the Colonial Secretary by stating that if the British Government would not concede any saving of cost on the Martini-Henrys and ammunition then he would be happy to accept Sniders instead. He meant of course Snider rifles as well as ammunition, but the War Office apparently concluded that he wanted the Martini-Henry rifles but the cheaper ammunition, which was Snider ammunition. This led to the Martini-Henrys being issued from the Tower in August 1873⁸⁰ and being received and issued in September 1874. Upon opening the ammunition crates they were found to contain Snider ammunition. Harvest complained in a letter to the Colonial Secretary which led to some somewhat strained correspondence between Western Australia and London. The Snider ammunition was transferred to the Enrolled Pensioner Force and on 22nd September 1874 approval was given to order 2000 rounds of Martini-Henry Ball ammunition and 2000 rounds of Blank ammunition from Melbourne "as a matter of urgency".⁸¹ These Martini-Henrys appear on the 1875 Returns where "82" are listed on issue to the Fremantle Rifle Volunteers, the extra ten rifles probably being Snider-Enfields.⁸² The *Inquirer* newspaper reported in May the following year that at a shoot, the F.R.V. would use "Sniders instead of Martini-Henrys"⁸³ indicating that they still had no ammunition eight months later. The Martini-Henry rifles would have been Mark I, (First or Second Pattern) arms,⁸⁴ but none have been noted. No mention of their marking was found. Interestingly, Harvest in 1876 offered these Martini-Henrys as a swap to the Pensioner "Day Force" in exchange for their Sniders, but London declined to permit it.⁸⁵ Harvest was attempting to regain uniformity of ammunition supplies (and bayonets) by having one pattern of service arm. Also, the greater number of secondhand Sniders to be had by swapping off the almost new and therefore more expensive Martinis would have allowed him to make up a shortfall he knew would occur when the order of Sniders per *Clifton* arrived in 1877. (Due to the small budget allowed him by the W.A. government the number of Sniders ordered was less than the number actually required for the volunteers). Instead of the swap the War Department agreed to sell W.A.

some Sniders at a discount. These discounted arms were the 33 Sniders per the *Eulic* in 1877. No other request for arms or ammunition is known until 1881 when a note stating "Issue 1200 rounds, Martini-Henry Ball ammunition to Capt. Sutherland"⁸⁶ was sent to the Enrolled Guard storekeeper Sgt. McCarthy, followed soon after by another which stated "Hand over to Captain Sutherland, commander of the Fremantle Rifle Volunteers, 20 Snider Rifles".⁸⁷ Increased enrolments had outstripped the Martini-Henrys, necessitating the issue of Sniders to supplement them. To redress the problem of two different patterns of arms being on issue in the corps about 28 Martini-Henry rifles were purchased "for the Fremantle Rifle Volunteers" in 1881.⁸⁸ No specific requisition document was found for this additional purchase but it is obvious from a Minute paper dated 15th January 1884 that this corps received the additional Martinis. Describing all the arms held by the F.R.V. as at 1st January 1884 it lists, "100 Martini-Henry Rifles, 100 bayonets", an increase of 28 Martini-Henrys since 1874. There is also a note stating that there were "50 Sniders (Converted Enfields), 47 Long and three Short in store".⁸⁹ These Snider-Enfields were obviously the standby arms already mentioned in the voucher of 1881 which were on loan from the E.P.F. The Commandants Report for 1885-86 shows that 20 additional Martini-Henrys were issued to the F.R.V. in 1886, bringing the total to 120 stand.⁹⁰ He also stated that "The rifles in possession of the Fremantle Corps are nearly all greatly in need of browning and general looking over". These rifles, most of which had been in service since 1874 were the oldest Martinis in the colony. Consequently on 8th August 1887 the Commandant ordered and received in the same year, spare parts for Martini-Henrys Marks I, II, III⁹¹ with which the arms of the Fremantle Rifle Volunteers, (and others), were serviced. This corps was armed with Martini-Henry rifles until 1895 when as C and D companies of the 1st Infantry Volunteer Regiment they were issued with 81 Martini-Metford Mark I rifles. By 1899 they numbered 216 men having been reorganised and increased by the addition of F company, still armed with Martini-Metfords. In 1900 this corps was absorbed into the Western Australian Infantry Brigade becoming the 2nd Battalion, when they were issued with 249 Magazine Lee-Speed rifles.⁹²

The *Guildford Rifle Volunteers* were a detachment of the Metropolitan Rifle Volunteers from 1872-73 until 1874 when they officially became the Guildford Rifle Volunteers in their own right. For the first few years "only very obsolete rifles were available".⁹³ They were partially armed with Metropolitan Rifle Volunteer Enfields in 1874, and in 1877 when the M.R.V. rearmed with

Sniders, the Guildford corps completed their arming with more Enfields which then became available.⁹⁴ Some of these Enfields were surplus E.P.F. arms. The Returns of 1875 show that it was armed with 49 Enfields rising to 53 in 1878.⁹⁵ A letter from Lt. Col. Harvest to Governor Ord dated 3rd May 1878 discusses the issue of Snider rifles surplus to the reduced Pensioner Force. Harvest wrote seeking the Governors signature to allow him to:

"...immediately arm the Geraldton and Guildford Volunteers with Snider Rifles and thus the entire Rifle Volunteer Force in the Colony will be completely armed with breechloaders".⁹⁶

The strength of the corps in 1878 was 53 and the number of Sniders would have matched this figure. Six years later a Minute of 1st January 1884 confirms this fact as it shows the corps had the following arms in store. "19 Rifles, Snider, Long, one Short. 31 Rifles, Snider, Converted, Long, Two Short. 11 Rifles, Enfield, Pattern 1853 (used for recruit drill)".⁹⁷ These documents confirm that Lt. Col. Harvest was successful in transferring the E.P.F. Snider-Enfields to the volunteer corps, they being first recorded in the Returns of 1880. The Minute of 1884 also illustrates the care taken in the records to separate the colonial purchased Sniders from the Snider-Enfield conversions on loan from the E.P.F. (ie. the Imperial government). Between 1878 – 1886 the number of Sniders on issue to Guildford fluctuated, but reached its highest number in 1882 when 76 were on issue.⁹⁸

This corps is recorded in the Commandants Report of 1886–87 as being issued with 60 Martini-

Henry rifles, with another 20 being supplied in 1887–88.⁹⁹ This gave a total of 80 Martini-Henrys on issue, but as the corps strength continued to rise to 133 (as at 31st December 1887),¹⁰⁰ the 53 Sniders listed in the Minute of 1884 were again pressed into service and remained on issue until eventually replaced by Martini-Metford rifles in 1895. The corps declined in numbers from about 1890 and in 1893 became E and F companies of the 1st Infantry Volunteer Regiment. In 1895, the Returns show 104 Martini-Metfords on issue. By 1898 the numbers had fallen to 45. In 1900 this corps was absorbed by the Western Australian Infantry Brigade when it became A company of the 3rd Battalion. At this time it was issued with 59 Lee-Speed Rifles.¹⁰¹

The **Geraldton Rifle Volunteers** officially began in 1877¹⁰² with 53 men. Wieck states that "they were armed with very obsolete rifles which were not replaced until years later".¹⁰³ The records show that initially they were armed with Enfields issued from the Metropolitan Rifle Volunteers in 1877, as in that year a charge of two pounds five shillings was debited to the M. R. V. for "Cleaning Enfields, Geraldton". It appears that the Geraldton corps did not retain their Enfields long as soon after the Harvest letter of 3rd May 1878, in which this corps was earmarked as one of two designated to receive surplus E.P.F. Sniders, a cost of two pounds ten shillings was debited to the Geraldton corps on 30th August 1878, for "Marking Arms".¹⁰⁴ It is uncertain which arms the debit refers to but taken together with the Harvest letter, the two references indicate that in 1878–79 this corps may have been issued some of the 33 new Sniders which arrived



Figure 15 The ownership marks of the W.A. Defence Force, 1898 – 1903. This mark, "W A/1043/D", is on the right side of the butt of a Martini-Enfield Mark I, W.A. Pattern rifle. These arms were issued almost exclusively to the W.A. Mounted Infantry between 1899 – 1901. (Photo D. Elford).

on the *Eulie* in mid 1877 as well as the surplus Enrolled Pensioner Force arms selected by Harvest. Only the new arms would have required marking, the E.P.F. arms being Imperial arms on loan, are thought prohibited from alteration. Perhaps these 1877 "second order" arms are those referred to in the debit charge, as the corps is listed as having 52 Sniders on issue in 1880.¹⁰⁵ A Minute dated 15th January 1884 lists the G.R.V. as having "46 Long Snider rifles, four Short Snider rifles and 50 lots of accoutrements". These accoutrements are described as "Old and unfit for daylight Parade".¹⁰⁶

The Commandants Report for 1886 shows that the Geraldton Rifle Volunteers were armed with 60 Martini-Henry rifles in that year.¹⁰⁷ In 1896 the G.R.V. were issued with 70 Martini-Metford rifles and in 1898 they were issued with 89 Martini-Enfields,¹⁰⁸ the Martini-Metfords presumably being re-issued to another corps, most likely including their mounted detachment. The Martini-Enfields were Mark I W.A. Pattern rifles, part of a lot ordered in 1897 and received in 1898.¹⁰⁹ These arms were marked on the butt "W A over number", possibly including the suffix "D" (see Figure 15). The arm in Figure 15 is from the W.A. Army Museum Collection (Item 082.90).

The G.R.V. are the only volunteer rifle corps known to have been issued any of these imported

Martini-Enfields, which can be seen in a photograph in Trotter⁷⁶, (p. 302). These W.A. Pattern Martini-Enfield rifles are considered unique among Australian colonial Martini-Enfield rifles as they alone fixed the Pattern 1888 sword bayonet. With the exception of a number of Queensland arms set up to take a side-mounted sword bayonet, all other Australian Martini-Enfield rifles took the Pattern 1895 socket bayonet, (see Figure 16). The G.R.V. retained these arms even after they became B company, 3rd Battalion, Western Australian Infantry Brigade in 1900.

In 1884, the Geraldton corps raised a detachment at Northhampton. It was a half-company known as the **Northhampton Rifle Volunteers**. They were armed with 40 stand of Sniders handed down to them by the Metropolitan Rifle Volunteers when this latter corps was issued with new Martini-Henrys. They retained these Sniders until replaced by 40 Martini-Henrys in 1887.¹¹⁰ The Northhampton Rifle Volunteers had become totally inefficient by 1899 and were disbanded that year.

The **Wellington Mounted Volunteers** were raised in 1877. It is recorded that "rifles" were shipped to Bunbury for them on 16th December 1878,¹¹¹ and they were reported as having used Enfield rifles in a "hot and windy" shooting match later in the month.¹¹² These rifles were probably not



Figure 16 The distinctive nose cap feature which makes the W.A. issue Martini-Enfield rifles unique. These rifles are the only Australian Martini-Enfield rifles which fix the Pattern 1888 sword bayonet. The upper rifle is the Martini-Metford Mark I, W.A. Pattern, the first W.A. service rifle to fix the Pattern 1888, the lower is the Martini-Enfield Mark I, W.A. Pattern. (Photo R. Sinclair).

the issue arms of the corps but rather target practice arms. Wieck states that they were armed with revolver-carbines like the Pinjarrah Mounted Volunteers,¹¹³ but the only records found show that they are recorded as being issued with "Swords and Belts" and "30 Pistols" in 1878.¹¹⁴ The Returns of 1880 – 1882 describe their arms as "Light Cavalry Swords and Revolvers". One of their swords, No. 34, is in the W. A. Museum Collection (W1182). The blade is etched with their name. They were disbanded in 1882, as, like the Pinjarrah Mounted Volunteers, they could only muster eight troopers that year. In a report on their disbandment the Commandant, Colonel Angelo, recommended that their commander, Captain Lovegrove and his men be permitted to "keep their rifles" on the understanding they started a rifle club at Bunbury. The request was granted.¹¹⁵

The **Albany Rifle Volunteers**, raised in 1878, were armed initially with 52 Pattern 1853 Enfield muzzle-loading rifles shipped from Perth per the *Rob Roy* on 23rd August 1878.¹¹⁶ It seems these Enfields were soon replaced by Sniders. In December 1879, a requisition was sent to acquire "50 Rifles, B.L. Snider. 40 Long butts, 10 Short butts, with bayonets and sword bayonets – for Albany Rifle Volunteers".¹¹⁷ These rifles arrived in 1880 and are shown on the Returns between 1880 – 1885. They appear in a photograph in Grant, (p. 29). The Commandant was making arrangements for ordering Martini-Henry arms for this corps when they were disbanded in early 1885.¹¹⁸ The disbanded corps was replaced two months later in May 1885 by the **Albany Defence Rifles**. Plans were finalized to requisition a quantity of new Martini-Henry rifles for them in 1885, the Commandant desiring particularly that the A.D.R. "...be supplied with the best Rifle".¹¹⁹ These rifles were issued in 1886. One of these Albany Defence Rifles Martini-Henrys survives in the W.A. Museum Collection (W535). It appears to be branded on the *left* side of the butt "A D R over 8" (see Figure 17). The use of the left side of the butt and branding have been noted as a standard alternative to engraving on the buttplate tang. This alternative was in British military usage at least in the first half of the nineteenth century.¹²⁰

This rifle is one of only three specimens of W.A. Martini-Henrys known to have survived. It is the third volunteer arm, (together with the Pinjarrah Mounted Volunteers revolver-carbine and the Metropolitan Rifle Volunteers Martini-Henry), known to have an individual corps mark. The 1886 Returns show the Albany Defence Rifles as being issued with 75 Martini-Henry rifles, part of 80 apportioned to Albany out of a large order of 250 received in Perth in that year.¹²¹ Again, this corps had to be disbanded in 1888 "and its arms returned to store".¹²² It was replaced by the **Plantagenet Rifle**



Figure 17 The ownership marks of the Albany Defence Rifles, 1885 – 1888. This mark is on the left side of the butt of a Martini-Henry Mark III rifle. It is thought to have been put on in Albany, indicating that some corps may have marked their own arms. (Photo D. Elford).

Volunteers. This corps received 62 of the Martini-Henrys of their predecessors which are recorded in the Returns of 1889.¹²³ The Returns of 1890 show this corps as being issued with 46 Martini-Henrys which they kept until 1895.¹²⁴ In 1896 they were issued with 48 Martini-Metfords,¹²⁵ used by them for musketry and drill and also in their capacity as relief gunners for the Albany coast defence artillery (Permanent Force). They were disbanded in 1897. Many members of the Plantagenet Rifle Volunteers became members of a new volunteer corps raised in 1899, the Albany Volunteer Garrison Artillery. These men also assisted with the manning of the coastal defence artillery, having 66 men by 1900.¹²⁶ Nothing was found concerning their firearms other

than a report in 1901 which stated that their "rifles" had arrived by train.¹²⁷

The **York Rifle Volunteers** were raised in 1878, after an extended period of uncertainty beset with financial and other problems. Wieck says in the preliminary stages of their establishment, "tentative approval was given for the loan of the muskets".¹²⁸ In 1878 or 1879 they evidently received the handed down Enfields of the Metropolitan Rifle Volunteers as initially proposed by Harvest in his letter of November 1875, because in the 1879 Returns they are armed with 41 Enfields. In 1884 their stores are listed as including "18 Muskets. 55 Rifles, Enfield, and 13 Rifles, Snider".¹²⁹ The Returns of 1885 list them with 33 Sniders, part of about 50 they received in 1884 from the Metropolitan Rifle Volunteers when this latter corps received its new Martini-Henrys.¹³⁰ They disbanded in 1886 before being issued with any of the Martini-Henrys. After a hiatus of seven years the **York Infantry Volunteers** were raised in 1893. They are shown in the 1893 Returns as being armed with 67 Snider Rifles,¹³¹ and in 1895 they were armed with 70 Martini-Metford rifles. They were re-named the York Infantry in 1899 and in 1900 they became D Company, 3rd Battalion, W.A. Infantry Brigade still armed with 60 Martini-Metford rifles.¹³²

The **Naval Artillery Volunteers** as they were known were raised as the Fremantle Naval Artillery Volunteers in 1879. They were reported to be armed with "carbines". Halls states that they were issued with Snider-Enfield two band Artillery Carbines in the 1880's,¹³³ while Skennerton states that the Snider-Enfield Naval Rifle was issued in Western Australia "to naval units".¹³⁴ The records show that on 1st December 1879 a requisition was forwarded to England to acquire "25 Carbines or Rifles, Naval Pattern 1858, Complete with sword bayonets, scabbards etc.". ¹³⁵ These naval rifles, which are very similar to the army short rifle, were received and were issued. The corps is listed in the Commandants 1881 Report as being armed with "Snider Rifle, 58. Naval Pattern."¹³⁶ This list is clarified further in 1884 when the corps is recorded as having in store "25 Rifles, Naval, 25 Cutlass bayonets",¹³⁷ and interestingly, under "Old Stores" were listed "25 Percussion Muskets with bayonets". This latter notation indicates that these old muskets and bayonets were issued at the time of raising and were their issue arms until replaced by the Sniders. Other archival evidence of arms which was found for this corps states that on 10th May 1881, Lt. Forsyth purchased four Sergeants swords at Lionel Samson's auction of the Enrolled Pensioner Guard stores. On the 12th May, Lt. Forsyth applied to the authorities to have the cost waived as he intended that they be used by the F.N.A.V. (Fremantle Naval Artillery Volunteers).¹³⁸

A Naval sword bearing his name and "Fremantle N.A.V." is in the W.A. Museum Collection (W75.50). In 1888 this corps which had been run on naval lines, was re-titled the **Fremantle Artillery Volunteers**, re-issued with army uniforms¹³⁹ and thenceforth run on army lines. On 30th May 1891 they were issued Martini-Henry rifles.¹⁴⁰ They became the No. 2 (Fremantle) Battery, Field Artillery in 1897. In 1898, according to Halls they were issued with "Martini-Enfield Carbines" and in 1900 received "Martini-Enfield Artillery Carbines Mark I".¹⁴¹ Skennerton states that "small numbers" of Martini-Enfield Artillery Carbines Mark I were used in Western Australia.¹⁴² No arms of the types described have been noted by the author as yet. The markings of all of these arms are also unknown. According to the 1900 Returns this unit entered the Commonwealth with 79 men on the roll.

The **Bunbury Rifle Volunteers** were raised in 1892 and according to the Returns of 1893 – 1894 were issued with 45 Martini-Henry rifles.¹⁴³ They received 74 Martini-Metfords in 1896 rising to 237 in 1900. This large issue of rifles included 133 for the four Divisions of the South-west Mounted Infantry, raised in that year. A contemporary newspaper account states that the Mounted Rifles had been armed with "...antiquated Snider rifles".¹⁴⁴ The B.R.V. became C Company, 3rd Battalion, W.A. Infantry Brigade on 3rd September 1900.¹⁴⁵

The **Perth Mounted Rifle Volunteers** were raised in 1894 and are noted as having 42 men in May of that year.¹⁴⁶ It is possible that this corps was also armed with "...antiquated Snider rifles". They are noted in the 1895 Returns as being issued with 31 Martini-Metford rifles. They do not appear again in the Returns and were disbanded in 1897.

The **Metropolitan Civil Service Battalion** was raised in December 1899. This unit seems to have suffered from some neglect, due to the raising and equipping of the various contingents to the Boer War. It was initially issued with W.A. Defence Force Martini-Henry Rifles converted locally to become .303 inch "Unofficial Conversion" Martini-Enfield Mark I rifles, W.A. Pattern, (see Figure 19). As the number of men in this corps in 1900 totalled 284, it is reasonable to assume that the Unofficial Conversions issued to them also totalled 284.¹⁴⁷ Specimens of these conversions noted were still marked on the butt with their original W.A.D.F. initials and stand numbers, no additional mark being applied at the time of conversion. The mark thought to have been put on the original Martini-Henrys in 1893 when the W.A. Volunteer Force became the W.A. Defence Force, consists of the letters "W A D F" within a 2 cm circle (see Figure 18).

A contemporary *Australian Advertiser* newspaper account (of the receipt of the new Martini-Metford



Figure 18 The ownership marks of the W.A. Defence Force. It is thought this mark was used between 1893 – 1895. The “W A D F” mark, contained within a 2 cm circle and struck from a single die punch, is on the right side of the butt of a Martini-Henry Mark III rifle, later converted to Martini-Enfield Mark I, W.A. Pattern to become the Unofficial Conversion. (Photo D. Elford)

rifles in July – August 1895), alludes to the proposed conversion of the remaining Martini-Henrys. It describes how:

“...at a comparatively light cost the military authorities will be able to alter the present Martini-Henri (sic) rifles by fitting them with Metford barrels”,¹⁴⁸

The Unofficial Conversion shown in Figure 19 is fitted with a replacement Enfield barrel, but a rifle fitted with a Metford barrel as described in the newspaper article has been noted. A rifle fitting this description is depicted in Figure 21. A careful study of the rifle in Figure 21 reveals that by the presence of the double step shape of the short Nock’s form at the breech, the barrel can be determined to be a Metford barrel.¹⁴⁹ No officially converted Martini-Enfields were produced with this type of barrel, therefore the rifle depicted in this contemporary 1900 photograph can only be one of the locally converted Unofficial Conversions. These Unofficial Conversions are the only Martini-Enfields which were fitted with Metford barrels, a fact which may also explain why these Martini-Enfields alone were fitted with the

superceded two-piece Metford type Rigby nose cap, rather than the then current one piece nose cap fitted to other appropriate British service arms. It is possible that although the barrel is of the Metford profile, the rifling, at this late date may have been of Enfield type, suitable for cordite. One of the two specimens of this locally converted Martini-Enfield, examined during the course of earlier research into these W.A. Pattern arms, was still fitted with the Metford profile barrel. Arms of this type, fitted with Metford barrels and converted locally from W.A. volunteer Martini-Henrys, match precisely the description of the proposed conversion arms given in the *Australian Advertiser* newspaper account of the proposed conversions on 28th August 1895.

It is certain that William Vernon Needham, gunsmith, of Lincoln Street, Highgate Hill performed these conversions, using parts supplied from England. Mr Needham came from an important line of English gunmakers. He emigrated to Sydney in 1875, setting up business in Paddington, where he is recorded as being in business in 1885.¹⁵⁰ He subsequently moved to



Figure 19 The Unofficial Conversion Martini-Enfield Mark I, W.A. Pattern. There is evidence that William Vernon Needham, a local gunsmith and Armourer to the Forces, did the conversions. This specimen, in poor condition, no longer has its original Metford profile barrel. (Photo D. Elford).



Figure 20 William Vernon Needham, "Armourer to the Forces", standing in front of his premises in Hay Street Perth. According to the Winchester Repeating Arms Company calendar visible in the window, this photograph was taken in January 1894, some six months after he received his government appointment. It was probably taken to commemorate the event, which is noted in his new sign, "By Appointment to the Government of W.A., Armourer". (Photo courtesy of Elizabeth Mansom.)

Perth and is recorded in various trade and postal directories as being in business in William Street in 1887, in Hay Street between 1888 and 1895, and at 101 Barrack Street and 44 Lincoln Street between 1895 and 1898. From 1898 until his death in 1928 he worked from number 44 Lincoln Street, then number 68, and finally number 70.¹⁵¹ Needham, a highly esteemed gunsmith, was appointed by the W.A. government as "Armourer to the Government Departments"¹⁵² in 1888, and "Armourer to the Forces" on 9th May 1893.¹⁵³ Operating from his Hay Street premises, (see Figure 20) he was retained to undertake the:

"Examination of Rifles including stripping, cleaning, oiling, correcting of sights, adjusting pull-off and refitting of damaged portions of locks etc., with parts supplied by the government".¹⁵⁴

During 1900 the pressures of arming the Boer War contingents was great, and it is thought that the arms of the Metropolitan Civil Service Rifle Volunteers may have been requisitioned for them, possibly leaving the M.C.S.R.V. unarmed for a short period, until the issue of the new Magazine Lee-Speeds could be arranged. In September 1900 the corps became the four companies of the 4th

Battalion of the Western Australian Infantry Brigade and are recorded as being armed with 284 Magazine Lee-Speed rifles.¹⁵⁵ The Unofficial Conversion Martini-Enfields which were handed in were reissued to W.A.M.I. Contingents to the Boer War. The M.C.S.R.V. corps and the Fourth W.A.M.I. (see Trotter⁷⁶, p.303), are the only units known to have received these arms.

The **Permanent Force** was not a volunteer corps. It was established by the agreement of most of the colonies in 1892 as a co-operative defence scheme, and in fact was a foreshadowing of the Federal defence scheme to come later. When the Permanent Force was set up it was intended that detachments would be posted to selected coastal defence sites in the various participating colonies. In W.A. Albany was chosen to have defensive coastal fortifications built and artillery installed. A crew of artillerymen was sent from South Australia in 1893 to man the guns. These men were armed with Martini-Henry artillery carbines (see Figure 22). In 1895 the W.A. Returns list 26 men for this Force and the Dominion Returns of 1904 list 26 Martini-Henry carbines in store,¹⁵⁶ indicating that these carbines remained in W.A. after they were retired. One



Figure 21 The Metropolitan Civil Service Rifle Volunteers in camp in 1900. Between December 1899 and mid 1900, the corps was issued with the Unofficial Conversion W.A. Pattern Martini-Enfield. Careful examination of the rifle in the original photograph reveals the short, two step Nock's form at the breech, a characteristic of the Metford profile barrel. Only the Unofficial Conversion Martini-Enfield had this feature. (Photo courtesy of History House Museum, Armadale. A.K.P. 661 C.9 A.5).

Martini-Henry artillery carbine in the W.A. Museum Collection (W175) is marked on the right side of the butt "P M F over 110" (see Figure 23). This carbine is accompanied by its Pattern 1879 bayonet also marked "110" (W.A. Museum W1099). The carbine is marked on the body "Broad arrow over S A over 541". The bayonet also bears the "Broad arrow over S A" ownership mark. The W.A. Government Gazette of 6th April 1893 gives the W.A. Permanent Force initials as "W.A.P.F." or "P.F."¹⁵⁷ The mark "P.M.F." therefore is definitely not a W.A. mark, standing in fact, for "Permanent Military Force", a South Australian variation.¹⁵⁸ It is tentatively suggested that this arm may be one of the 26 Permanent Force carbines brought over from South Australia by the gun crew in 1893. A second Pattern 1879 bayonet in the W.A. Museum Collection (T418), is also marked with the South Australian property marks and bears stand number "97", confirming that a number of these arms once existed here. From these stand numbers it can be deduced that the South Australian carbines and

bayonets include the numbers spanning "97 – 110", potentially identifying 14 of them. The circumstantial evidence presented to connect this arm with Albany is very strong, but whether this arm is definitely linked to Albany must await verification.

There is reasonable evidence to conclude that the Permanent Force was issued with rifles in the 1898 – 1900 period when the Martini-Henry carbines were retired. One firearm noted during research for *The Martini-Enfield Rifle in Western Australia* was a Martini-Enfield Mark I W.A. Pattern rifle, marked on the butt "W.A.A. over 7" (see Figure 24).¹⁵⁹ This mark, adopted in 1893, is the identification letter code of the "Western Australian Artillery", which was the artillery company of the Permanent Force. The W.A. Government Gazette of 6th April 1893 stipulated that the shoulder straps of the Permanent Force uniform would have as identifying initials "W.A.E. for the Engineers and W.A.A. for the Artillery".¹⁶⁰ A requisition for artillery pattern uniform buttons and badges, and



Figure 22 The Permanent Force at Albany, 1895. These men were recruited in South Australia and brought Martini-Henry artillery carbines and Pattern 1879 bayonets with them when they came. These arms can be seen in this photograph. (Photo courtesy of Army Museum of W.A.).

sleeve and shoulder insignia depicting the initials and words "Western Australian Artillery", was sent on 19th May 1893.¹⁶¹ This requisition was for the NCOs and men of the Permanent Force. The recorded use of the letters "W.A.A." on the uniforms of this unit which have also been noted

as being present on this rifle, a pattern of arm unique to W.A., is undoubtedly the evidence necessary to connect the two. This evidence points to the W.A. Artillery being issued with *rifles* c.1898, rather than more modern types of artillery carbines. It is therefore possible that other artillery



Figure 23 The ownership marks of the Permanent Military Force of South Australia. Men were enlisted in South Australia as gun crew in 1892 and commenced service in Albany in February 1893. It is thought this carbine is one of 26 of these Martini-Henry artillery carbines which were brought with them at this time (Photo D. Elford).



Figure 24 The "W.A.A." ownership marks of the W.A. Artillery company of the Permanent Force which manned the Albany fortifications, 1893 – 1901. The mark is on the right side of the butt of a Martini-Enfield Mark I rifle, W.A. Pattern. (Photo R. Sinclair).

units may also have been issued with rifles at this time, but as yet none have been noted.

The brief period from 1895 through Federation to 1903 saw the reforming of existing corps and the raising of new corps which took the W.A.D.F. into the Commonwealth. Corps of this era included the Pinjarra Mounted Infantry, Goldfields Battalion of Infantry, W.A. Mounted Infantry (W.A.M.I.) and the Boer War W.A.M.I. Contingents. It was a period of rapid expansion in the numbers of men and arms. This expansion, from 617 NCOs and men in 1895 to 2561 NCOs and men in 1900,¹⁶² naturally led to a huge increase in the demand for arms.¹⁶³ Additionally, there were 872 NCOs and men in the six W.A.M.I. Contingents to South Africa also requiring arms. The words of the Local Commandant of the time, Col. Chippindall, sum up the pressures of this phase in the life of the Defence Force. He wrote:

"No separate Department exists for Pay, Stores, Supplies, Commissariat, Transport, Medical etc. etc., and (if one realises) that all details are carried out in one office, some idea of the work done can be arrived at".¹⁶⁴

Because of the continuous raising and despatching of troops, the movements of arms between corps and the almost complete absence of records for this period, the arms and their marks are described now as a group rather than by issue to individual units. To maintain continuity the subject is discussed from 1895 – 1903.

On 17th January 1893 the W.A. Government ordered 700 Martini-Metford Mark I Rifles, W.A. Pattern. The W.A. Pattern refers to the fact that these rifles were especially modified for W.A. by the inclusion of a butt-trap for the oil bottle and sighting for black powder .303 inch cartridges. This arm was the first of a line of W.A. Pattern Martini arms which fixed the Pattern 1888 sword bayonet instead of the socket bayonet previously utilized by the Martini-Henry rifles in service.¹⁶⁵ These 700 rifles arrived in 1895 and issue began immediately, the newly established First Infantry Volunteer Regiment being armed first, with the York Infantry and the Perth Mounted Rifles also receiving their arms in that year.¹⁶⁶ Specimens of Mark I examined confirm that these arms were stamped with a simplified ownership code, "W A over number" (see Figure 13). They were marked from 1 – 700. In 1897 a further 200 Martini-Metford rifles were purchased from England. This time however, they were the Mark II type, unable to fix the Pattern 1888 sword bayonet, taking instead the Pattern 1887 sword bayonet, an entirely different bayonet which would have to be specially ordered. There is tentative evidence to suggest that these Mark IIs may have been ordered due to a lack of military knowledge on the part of the civilian purchasing agent in London. He may have just ordered "more" Martini-Metfords, without knowing there was a Mark II variation, a type different from the Mark I previously supplied. In



Figure 25 The Martini-Enfield rifle, Mark I W.A. Pattern. This arm is one of 1150 Mark I and II rifles shipped from the Tower of London between 1898 – 1901. (Photo D. Elford).

fact, in an attempt to have the vacant position of Military Adviser filled, the Agent General's Report of 1899 stated:

"The passing of military stores is something that can only be described as chaotic. A Military Adviser could assess the difference between MK I, II, III which is of considerable importance to the military but which is of no importance to a civilian"¹⁶⁷

These Martini-Metford arms were all issued to the Volunteers initially and many were later taken to South Africa by the Boer War Contingents. It is thought that the Mark IIs were modified to fix the Pattern 1876 socket bayonet of the retired Martini-Henrys, now in store.¹⁶⁸ No specimen of the Mark II is known to have survived but it is thought probable that the simple "W A over number" mark was continued, and they were numbered 701 – 900.

Following close upon this acquisition came a quantity of Martini-Enfield Mark I rifles, W.A. Pattern, obtained from the War Office in England. These rifles were essentially the same as the Martini-Metford Mark Is of 1895 except for a three inch shorter barrel made with Enfield rifling to accommodate the new smokeless cordite powder, rather than Metford rifling which was adapted to the earlier black powder cartridges. As W.A. still had considerable stocks of black powder cartridges, these Martini-Enfields were sighted for these rather than the cordite type. The W.A. Pattern Martini-Enfield, in common with the Martini-Metford Mark I, had a Rigby type nose cap fitted which allowed the fixing of the Pattern 1888 sword bayonet (see Figure 16).¹⁶⁹ No documentation was found for this 1898 shipment other than records for 200 Martini-Enfield Mark Is (presented by the author in a previous paper),¹⁷⁰ but an undated, unsourced list showing that "900 Converted Rifles" were issued to W.A. from the Tower in May 1898 "on ordinary repayment"¹⁷¹ has been determined to refer to a considerably larger shipment of Martini-Enfields than previously thought. The list indicates that 900 Martini-Enfields (which may include Mark II W.A. Pattern arms) arrived here in 1898. The list also shows "200 Converted rifles" sent to W.A. in May 1900, "on special repayment" with another "50 Converted rifles" issued in October 1901 "on ordinary

repayment". There is no doubt that the description "Converted rifles" refers to Martini-Enfields as these arms were conversions of Martini-Henrys, while the Martini-Metfords previously mentioned were all new-made arms. These revised figures increase the previously known total from 400 M-Es received between 1898 – 1900 to 1150 received between 1898 – 1901. Examination of surviving arms has revealed that all were converted at the Royal Small Arms Factory at Enfield in England, all were W.A. Pattern fixing the Pattern 1888 sword bayonet, and both Mark I and Mark II types were included. Butt stand numbers support the larger 1150 total being correct as the highest stand number noted was 1057.

The first Martini-Enfields arrived in 1898 and a small number, 89, were issued immediately to the Geraldton Rifle Volunteers, the only volunteer corps known to have received them. An estimated 30 were also issued to the W.A. Artillery company of the Permanent Force at Albany. The volunteer force being fully equipped with Martini-Metfords, the remainder of the Martini-Enfields were issued in response to the huge demand to equip the escalating enrolments in the W.A. Mounted Infantry and the Boer War W.A.M.I. Contingents between 1899 – 1901. At this time the demand for arms became so great that many of the Martini-Metfords of the volunteers were withdrawn and, with these Martini-Enfields, were issued to the mounted contingents. The Martini-Enfields used by these units were stamped on the right side of the butt "W A over number over D" (see Figure 15). Butt numbers noted indicate that the arms were numbered from 1 – 1100 D. Many of the Martini-Metfords and these Martini-Enfields went with the Contingents to South Africa and possibly never returned.¹⁷²

In addition to these imported Martini-Enfields a quantity of W.A. Defence Force Martini-Henrys were converted locally in Perth into Martini-Enfield Mark I W.A. Pattern rifles from parts supplied from England in 1899 – 1900 (see Figure 19). The exact number is uncertain but is around 251 – 284.¹⁷³ These arms were pressed into service with the Metropolitan Civil Service Rifle Volunteers as soon as they could be converted and



Figure 26 The ownership marks of the W.A. Defence Force, 1900 – 1901. The mark is on the right side of the butt of a Martini-Enfield Mark II, W.A. Pattern. This mark does not include the suffix "D", found on the earlier Martini-Enfields. It is not known to whom these arms were issued. (Photo D. Elford).

some are known to have been subsequently issued to the Boer War Contingents.

The Boer War demand on the Volunteer Force's supply of arms was intense, with many of the volunteer corps finding it difficult to maintain their own arms needs. By early 1900 it was reported that:

"Consequent on the distribution of rifles amongst the different Western Australian contingents, the local defence force has found it necessary to replenish its stock of firearms. The Premier recently despatched an order to England for a supply of rifles."¹⁷⁴

This order for the local defence force included 1000 Magazine Lee-Speed rifles which arrived in 1900, and also the 200 Martini-Enfields of 1900. By December 1900, 821 Lee-Speeds were on issue to the W.A. Infantry Battalion. The First Battalion at Perth had 229, the Second at Fremantle had 249, the Third, (one company), at Guildford had 59 and the Fourth (Civil Service) Battalion of four companies had 284 rifles on issue in Perth.¹⁷⁵ Perhaps the very last of the purely colonial arms

purchases were 50 Martini-Enfields which were sent to W.A. in October 1901.¹⁷⁶ It is a very difficult matter attempting to identify this shipment among the other 1100 M-Es sent from England between 1898 – 1900, but a number of Mark II rifles dated 1900 have been noted marked "W A" in large letters without the "D" suffix. On these rifles the stand number has been placed at some distance from the letters (see Figures 26 and 27). It is possible that the 50 arms of 1901, not arriving until after the sixth and last W.A.M.I. Contingent was sent to South Africa, were issued to some other group and therefore were marked differently, not having the "D" suffix. The arm illustrated in Figure 26 may be from this shipment. From this time onwards all arms purchases for the states were by the Commonwealth Government, the states having handed over all defence responsibilities in the 1901–1903 period.

In June 1903 a shipment of 1350 Magazine Lee-Enfields were sent (W.A. Museum F87.046). These



Figure 27 The Martini-Enfield rifle Mark II, W.A. Pattern. One of the 1150 Mark I and II rifles shipped here from the Tower between 1898 – 1901. The rifle still has its spring steel foresight protector in place. (Photo D. Elford).



Figure 28 The butt marks of an early Commonwealth period Magazine Lee-Enfield Mark I*. The stand number, and the Commonwealth roundel with "W A" in the centre, are visible, as are the manufacturer's roundel and the twin opposing broad arrows denoting sale. This rifle also bears marks indicating issue in April 1906. The stand number and the letters "W A" are repeated on the breech. (Photo D. Elford).

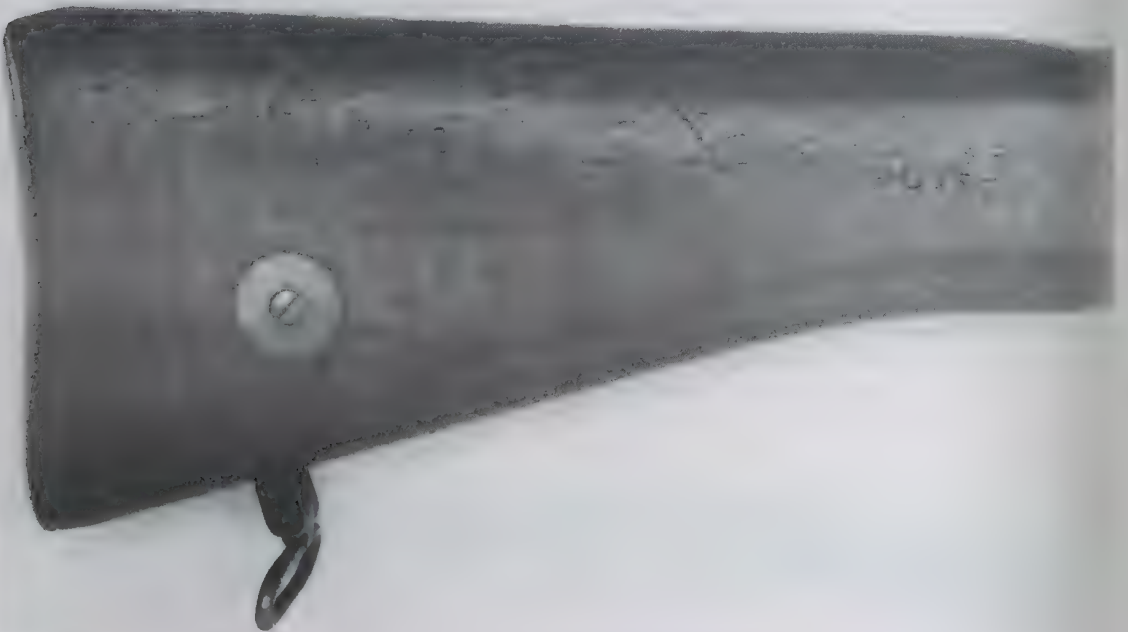


Figure 29 Butt marks of an early Commonwealth period Short, Magazine Lee-Enfield Mark I. The Commonwealth roundel with "W A" in the centre, the stand number and the August 1906 issue date are visible. This arm is one of 600 ordered in 1904. (Photo D. Elford).



Figure 30 The breech of the arm illustrated in Figure 29, showing the stand number and the "W A" mark denoting Western Australian issue. (Photo D. Elford).

and other identical arms were marked on the breech of the barrel with "W A" and the stand number. The "W A" was struck with a single two letter die punch. "W A" and the stand numbers were also struck on the left side of the butt, but now the letters "W A" were surrounded by a circle containing the words "Commonwealth of Australia Mily. (military) Forces" (see Figure 28). Stand numbers noted have been in the 2000 – 3000 range. These arms are not marked to units so it is not possible to identify specific issues.

Army General Order 289 of 16th February 1903 and General Order 15 of 20th January 1904 give the requirements for marking Commonwealth arms. The regulations give the example "A over 10 over A.I.R." (A Company, 10th Regiment, Australian Infantry Regiment),¹⁷⁷ which for W.A. would be "A

over 11 over A.I.R.". Arms have been noted marked this way for eastern states regiments but as yet none have been noted for W.A. In 1905 W.A. received around 600 Short, Magazine Lee-Enfields Mark I (W.A. Museum W87.1).¹⁷⁸ These arms were marked in an identical manner to the Magazine Lee-Enfields of 1903 (see Figures 29 and 30), and also do not have the "A.I.R." markings stipulated in the 1903–04 orders. The SMLE Mark Is were issued in 1905–06 with stand numbers from 1 – 600, those noted have all been below 600. Other than state ownership marks there is nothing to indicate specific unit issue, the brass marking discs on the butts being left unmarked.

The Boer War period and the rapid expansion in the number of men and arms ushered in the era of modern armies and National Service. It was the



Figure 31 The butt marks of an early Commonwealth period War Office Pattern .22 inch training rifle. The marks indicate issue to the Citizen Military Forces of the 5th Military District, i.e., Western Australia. (Photo D. Elford).



Figure 32 The breech of the rifle illustrated in Figure 31, showing the repeated stand number and issue marks for Western Australia. (Photo D. Elford).

end of the old Volunteer Force and the beginning of the end of individual colonial identity in the military. In 1911, in conjunction with the other states, Western Australia was designated as the 5th Military District of Australia. From this time onwards the only identifying mark to indicate W.A. issue was the numeral "5", used either by itself or as "5th M.D.", "5 M.D." or "D arrow D over 5", (Defence Department). These marks appear mainly on Citizen Military Forces (C.M.F.) arms from this period, like the War Office Pattern .22 inch Training Rifle (see Figures 31 and 32) from the W.A. Museum collection (NA.52).

Pattern 1907 bayonets have been noted bearing Militia ownership numerals such as "16", "84" and "86", for respectively, the 16th Battalion, the Goldfields Infantry and the 86th Infantry. No such unit identity marks have as yet been noted on W.A. rifles, but individual unit identification marks such as "4 LH", "56 IB" and "24 IB" for respectively, the Fourth Light Horse and the 56th and 24th Infantry, have been reported to the author from the other states. Apart from the "A.I.R." marking already referred to, the regular army seems largely to have refrained from using state identity marks on arms, the numeral "5" alone surviving into more recent times.

THE CADETS

The W.A. Cadet Force is relatively unknown. In the 1861 – 1892 period the terminology "cadet" and "recruit" was used interchangeably, with the meaning seeming to imply recruit. The early Volunteer Corps are recorded as establishing their own Cadet Corps at Guildford, Perth and Fremantle. In 1883 they were issued with what were described as "Enfields, shortened in length" and in 1888 "short (Snider) rifles".¹⁷⁹ From 1888

they also utilized a sub-calibre device known as the Morris Tube which was inserted into the barrel of an existing arm and allowed the firing of smaller cartridges.¹⁸⁰ These Morris Tubes allowed the use of service arms for training recruits and cadets. In 1892 the W.A. Government began moves toward the establishment of a recognisable boys and juveniles Cadet Corps by introducing military drill into the schools. The Commandants Report for 1896 recommended that a Cadet Force be formed. He recommended that the senior cadets were to be armed with a suitable arm, while the junior cadets were not to be armed (i.e., dummy rifles only). They were to be provided with Glengarry cap, red serge coat, trousers and brown belt.¹⁸¹ Albany had attempted to raise a corps in 1895. Their junior cadets were issued with dummy rifles and Martini-Henrys were applied for to arm the senior cadets, but little more is known.¹⁸² In February 1897 Cadet Corps were established at Perth and Fremantle. The Commandants Report for 1898 recommended that Martini-Enfield Carbines be ordered for the Senior Cadets and dummy rifles for Junior Cadets, "as soon as a pattern is approved". His successor, in his Report for 1899 states that these arms had not been ordered and the cadets were drilling without arms. Again, in 1900 the Commandant reported that a corps of 50 Cadets had been raised in Coolgardie and that

"it would be a help if they could be issued with dummy rifles or M-E Carbines. These weapons have been asked for on several occasions and are asked for again."¹⁸³

It seems this lack of arms for the cadets may have continued through until after Federation in 1901. Treasury records show that funds for "rifles for Senior Cadets and dummy rifles for Junior Cadets" for the 1897–98 year were voted but were unexpended, the reason being "rifles not received

at close of year". The funding vote was repeated in 1898–99 but again was unexpended. In 1899 – 1900 no funds were voted for cadet arms. In the 1900 – 1901 year funds were voted for "cadet rifles, 500 with bayonets, and 500 dummy rifles". These funds were unexpended by 1901 – 1902 because "these votes lapsed upon transfer of the department to the Commonwealth".¹⁸⁴ Apparently the cadets languished somewhat between 1898 – 1903 and little activity is recorded for this period,¹⁸⁵ the non arrival of the 500 rifles and bayonets before Federation prevented weapons drill or musketry until 1903. The following Education Department records show that 1903 was the real beginning of the W.A. Cadet Force. Under the heading "Cadets and Military Drill" the 1903 Education Department Report states "The Cadet Force was brought into



Figure 33 The ownership marks of the W.A. Cadet Force. This mark consists of stand number "1144" over the initials "W A C F". The mark is located on the right side of the butt of a Francotte Martini cadet rifle. Between 1903 – 1904, around 1500 of these arms were issued by the Education Department of Western Australia. (Photo D. Elford).



Figure 34 The left side of the butt illustrated in Figure 33 showing the Western Australian Government ownership mark. (Photo D. Elford).

existence by the regulations which came into force on the 20th February", (1903). The first year was spent organizing the students and teachers in 27 schools so that by 31st December 1903 the department had 1208 cadets. The Report continued with a reference to arms, "The Force has been armed with Francotte rifles, and 1000 of these rifles have been obtained", but no ammunition accompanied the rifles and "regrettably" the cadets had been unable to practice musketry. The Report recommended another "500 Rifles and belts etc." be ordered in the coming year.

The arms referred to are the .297/.230 inch calibre Francotte Martini. The bayonet is a small socket bayonet. (W.A. Museum W1339). From the Education Department Report of 1903 it can be determined that the 500 rifles and bayonets ordered by the colony of W.A. in 1900 – 1901 was increased by another 500 rifles in the Commonwealth period 1902–03. According to the 1903 Report this increased order arrived in 1903 and was issued in one lot of 1000. It is concluded that the additional order of "500 rifles and belts" recommended for purchase in the 1903 Report also arrived soon afterwards, probably in 1904. This



Figure 35 The Western Australian Government ownership stamp impressed on the left side of the body of the Francotte Martini rifle discussed in Figure 33. This mark, along with the Francotte patent mark were impressed by the factory at the time of manufacture. (Photo D. Elford).

conclusion is supported by the serial numbers on these rifles. Arms have been noted in two serial number ranges, 61,000 and 67,000, indicating two separate groups. The first group, containing the expanded order totalling 1000, falls into the 61,000 – 61,999 serial number range. Butt stand numbers

noted in this range have all been between 1 – 1000. (The lowest 90, the highest 931). The arrival of the second group of 500 rifles recommended for purchase in the 1903–04 year is supported by another group of rifles noted as falling into the 67,000 serial range. The rifles in this serial range all



Figure 36 Southern Cross cadets armed with dummy rifles. This photograph was taken about 1904. (Photo courtesy of Army Museum of W.A.).

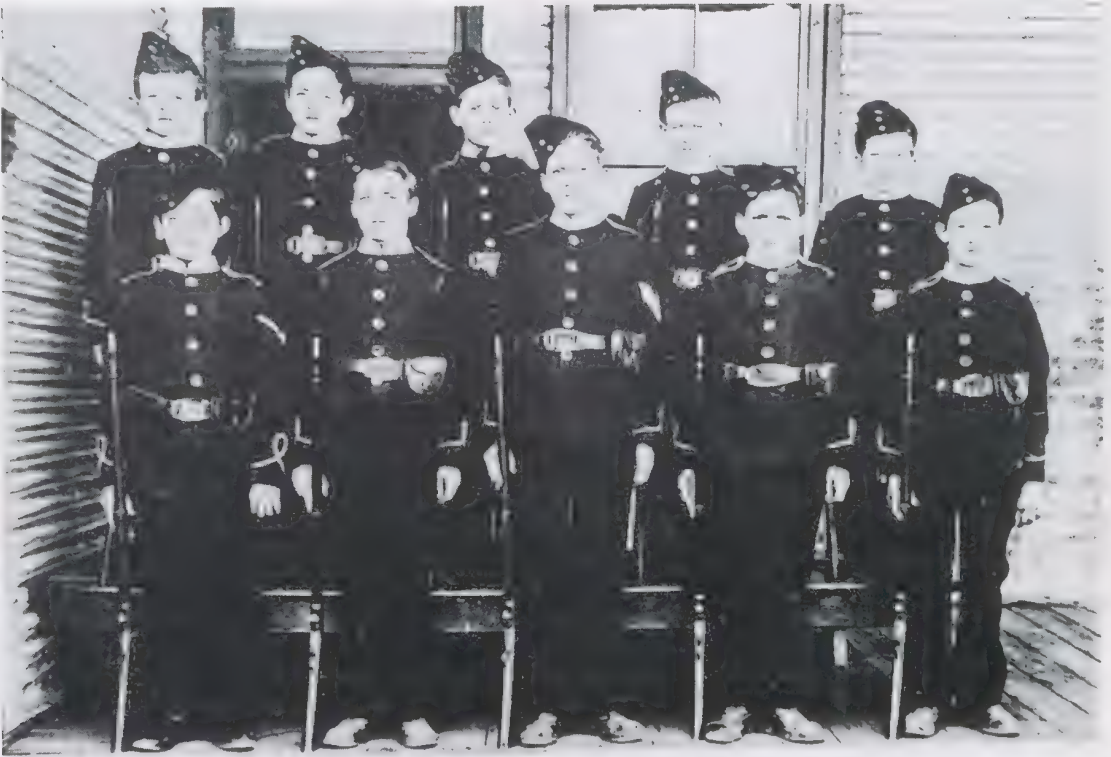


Figure 37 Cadets of the Trafalgar corps of 1904 armed with Francotte Martini rifles. (Photo courtesy of the *Kalgoorlie Miner* and Eastern Goldfields Historical Society. 21/28A).

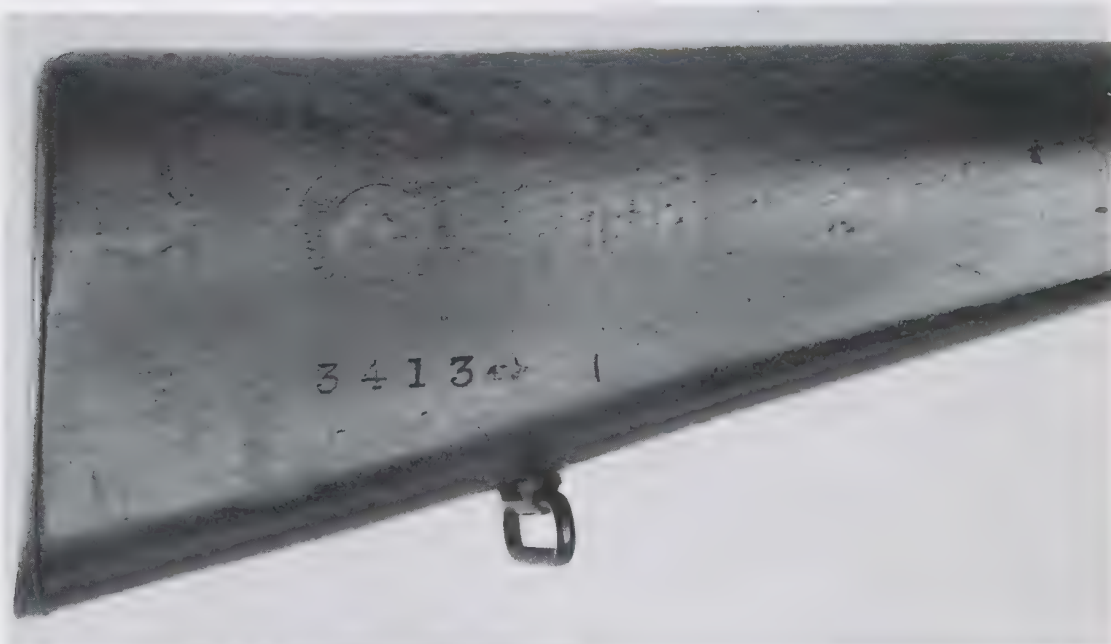


Figure 38 Commencing around 1908 the Commonwealth took control of the Cadet Force. This .310 inch Cadet Martini is marked on the right side of the butt with the Commonwealth ownership roundel with "W A" in the center and the stand number. (Photo D. Elford).



Figure 39 The right side of the body of the cadet rifle illustrated in Figure 38. The impressed Commonwealth of Australia ownership mark is evident as are the "W A" issue letters and stand number, 3413, punched in at the time of issue. (Photo D. Elford).

have stand numbers above 1000, (the lowest 1006, the highest 1144). The stand numbers indicate that the total number of rifles may only be 200, (the highest serial number noted was 67,176), but as 500 were ordered it is presumed that they all arrived and were issued. This physical evidence confirms that two lots of rifles arrived, were numbered with stand numbers continuing in numerical sequence, and based on present evidence totalled at least 1200. It is expected that further research will confirm that these cadet rifles did indeed total 1500. All Francotte cadet rifles are marked on the right side of the butt "number over W A C F". On the left side of the butt and body will be found stamped (by the factory), "Government of Western Australia" around a crown (see Figures 33, 34, 35). The W.A. Museum holds one of these rifles (W542).

Around 1908 – 1909 slightly larger Cadet Martini rifles of calibre .310 inch, made by W.W. Greener and Birmingham Small Arms were issued here, possibly replacing the Francottes. These later rifles were marked "W.A." on the right side of the butt and body, however the "WA" on the butt was surrounded by a circular stamp marked "Commonwealth of Australia Mily. (Military) Forces" (see Figures 38 and 39). The W.A. Museum holds two of these rifles, W1691 and W72.71. According to records, senior cadets may have been issued with Martini-Enfield .303 calibre rifles after 1903 and Magazine Lee-Enfields after 1908, but as yet, no arms have been noted so marked.¹⁸⁶

REVIEW OF PROCUREMENT AND ISSUE

The procurement and issue of volunteer arms to individual corps has been documented as far as the

surviving arms and the archives found allow. It is relevant now to examine the broader aspects of the procurement of these arms in terms of their "type" and total quantities.

As has been stated, the early Imperial arms of the garrison troops and the Enrolled Pensioners are known, but in general terms only. The apparent lack of identifying marks and possibly also stand numbers frustrates the accurate identification of these arms or their quantities. In the case of the garrison troops, it is certain that in most cases their arms departed with them when the period of their posting ended. It is not possible to estimate the quantities or types of arms they left in store at the time of their departure until new records are discovered.

The early Pensioner arms have thus far been referred to only as "smoothbore muskets" or "Carbine, Muzzle Loading". Considering the time frame of this early 1850 – 1860 period however, it is reasonable to assume that the Pattern 1839 and 1842 would have been included in their armoury. Of the bayonets from this period examined, the Pattern 1839 and 1842 are strongly represented, indicating their presence here in reasonable numbers. These smoothbore muskets survived in outstation service until 1881 when they were sold to the public.

It is not until the re-arming of the Pensioners with Enfields in c.1860 that a clearer picture emerges. It can be determined that the Enfields probably numbered around 300. This estimate is based on the numbers of Pensioners actually bearing arms as given in Broomhall's work, *The Veterans*. From this source it can be determined that the total of men under arms never seems to have

been more than about 300, a total which is supported by the highest stand number noted on an Enfield, number 260, and 167 on an Enfield bayonet. Taken together, these factors of evidence give circumstantial support for a probable total of 300 Enfields.

After transportation of convicts ceased in 1868, the need for the Pensioners gradually lessened over the following decade. In 1870, when this force was re-armed with Snider-Enfield rifles it is estimated that the need had declined considerably so that on this occasion only about 250 Snider-Enfields were received.¹⁸⁷ The highest stand number noted on an E.P.F. Snider-Enfield was 194.

The Volunteers, as has been noted, were issued with 200 Enfield rifles in August – September 1862 which seems to have fulfilled their requirements until the 1870's. They received a large quantity of Enfields from the E.P.F. when that body was re-armed with Snider-Enfields in 1870. It is not thought that they received all the E.P.F. arms as some small quantities of Enfields were still in the E.P.F. store when they disbanded in 1880. Enfields remained the issue arm of the Volunteer Force until they began to be replaced by Sniders in 1877. They were finally recommended for "abolition" in a letter from the Colonial Secretary to the Governor on 25th April 1882.¹⁸⁸ This recommendation was echoed in the Commandants Report of that year where he recommended that the "muzzle-loaders" should be sold.¹⁸⁹ The last corps to be armed with Enfields were the York Rifle Volunteers, who had them until 1883–84.¹⁹⁰ From this information it is evident that the volunteers had 200 of their own Enfields and the use of close to 300 others. The total number of Enfields in W.A. therefore was around 500.

In 1875, W.A. applied to England for a loan of 400 Sniders for the Volunteers but this was refused.¹⁹¹ The first Sniders received by the Volunteers were 111 long and seven short Sniders purchased by the Colonial government and issued to the Metropolitan Rifle Volunteers in early 1877, followed by 33 more in mid 1877. The Fremantle Naval Artillery Volunteers received 25 Pattern 1858 Snider Naval rifles in 1879 and the Albany Rifle Volunteers were issued 50 Sniders in the same year, (a contemporary account describes them as conversions). The colonial purchased Sniders therefore totalled 226. By 1881 Geraldton and Guildford both had about 130 Sniders between them, the volunteers having obtained access to the Snider-Enfields of the now disbanded Enrolled Pensioner Force. The Sniders and Snider-Enfields were the issue arms of the Volunteer Force until 1884 when they began to be replaced by the Martini-Henry rifle. In 1885 a shipment of spare breech-blocks and other parts for the Snider rifles was ordered for W.A. These parts were used in

1886–87 to "overhaul and put in thorough repair" 288 Snider rifles¹⁹² which were then kept as reserve arms in racks in the armoury at the Perth Barracks. This total did not include "40 issued to the York rifle club and 12 Short rifles to Major Gardiner for the use of the Cadet Corps". The Sniders were officially "called in" in 1887.¹⁹³ An Annual Return sent to the War Department in England in 1889 shows that W.A. had 366 Sniders and 104,790 rounds of ammunition in reserve as of 31st December 1888.¹⁹⁴ This Return confirms the totals of Volunteer and E.P.F. Sniders. By adding the 53 Snider rifles known to have been on issue at this time to the Guildford Rifle Volunteers, (between 1884 – 1895),¹⁹⁵ 12 with the cadets, 40 with the York Rifle Club, the 366 total increases to 471. Similarly, adding the 226 known Volunteer Sniders to the 250 Snider-Enfields of the E.P.F. gives a total of 476, which, allowing for a small unexplained discrepancy of five rifles between the two totals, thus reconciles the respective figures and establishes the total for Sniders in W.A. at around 470. Sniders were still on issue to the Guildford corps as late as 1893–94,¹⁹⁶ years after the Martini-Henry had superseded them throughout the Defence Force. According to an already quoted newspaper report, it was a shortage of modern arms which led to the arming of mounted units with Sniders in the 1894 – 1895 period.

It will be remembered that the Fremantle Rifle Volunteers were the first corps to be issued Martini-Henrys. They consisted of 72 Mark Is issued in 1874, with the total rising to 100 by 1881. The Commandant, obviously becoming aware of the desirability of re-equipping with this modern arm wrote in his Report as early as 1881 that:

"A large proportion of the Sniders are Converted Enfields and many of them are damaged and unserviceable. I would therefore submit for His Excellency's consideration, that it would be better to replace them by degrees with Martini-Henrys and that a supply of the latter be at once ordered for the Metropolitan Rifle Corps".¹⁹⁷

These arms were ordered in August 1883 but did not arrive for issue until 1884. They were 110 rifles "latest pattern" (Mark III). In 1885 another large order was sent from England. This order was for 101 Mark II rifles. They were intended for the Albany Rifle Volunteers, the "increased" Fremantle Rifle Volunteers and the Guildford Rifle Volunteers.¹⁹⁸ (It is possible that this order is actually part of the later, large order of 250). During the 1886–87 year 250 Martini-Henry Mark III rifles were received and were distributed to the Perth (30), Fremantle (20), Guildford (60), Geraldton (60), and Albany (80) Corps,¹⁹⁹ leaving only 60 more required to fully arm the Defence Force with Martini-Henrys. These 60 arrived in 1887 and were distributed to the Northampton

Rifle Volunteers (40) and the Guildford Rifle Volunteers (20).²⁰⁰ These seem to be the last purchases of Martini-Henrys made. Even though the demand for arms continued to increase, obsolete "reserve" Sniders were re-issued instead of further purchases of the Martini-Henry being made. The W.A. government attempted to obtain a gift of 1000 Martini-Henry rifles and bayonets from the Imperial government in 1892²⁰¹ but by 1893 it had become obvious that the British Government would not accede to this request. W.A. therefore commenced the procurement program of the new smallbore .303 inch calibre Martini arms. In an Annual Report to England in 1888 the total number of Martini-Henrys in W.A. was given as 574.²⁰² This total is repeated ten years later in the Commandant's Report for 1898-99,²⁰³ the rifles having been called in in 1896-97.

In 1893 the W.A. government began to procure what was to become a unique series of W.A. Pattern Martini .303 inch arms. This program began with the arrival of 700 Martini-Metford Mark I rifles in 1895. These arms were issued to the entire volunteer corps, the Martini-Henrys being retired. A further 200 Martini-Metford Mark IIs arrived in 1897-98, followed by 900 Martini-Enfields in 1898. 200 more Martini-Enfields arrived in 1900 with 50 more, the last, arriving in 1901. A further lot of around 251 - 284 Martini-Enfield arms were converted locally in Perth in 1899 - 1900. The imported M-Es were issued throughout

the mounted corps, with some of them going to the rifle volunteers at Geraldton and the W.A. Artillery company at Albany. The 251 - 284 local Unofficial Conversions went to the Civil Service corps in 1899-1900, and thence to the W.A.M.I. Many of these arms (272 M-Ms and c.606 M-Es), went to South Africa with the Boer War Mounted Infantry Contingents and possibly never returned.²⁰⁴ After the war Army General Order 296 of 24th December 1903 directed that all Martini-Enfield, Martini-Metford and Martini-Henry rifles still held in country areas were to be boxed and sent by rail to the central ordnance store in Perth. This was the final "call in" of the .303 inch Martini arms, as soon after, Army General Order 26 of 18th February 1904 began to offer for sale to the local rifle clubs "Martini-Henry, old 10/-, Martini-Enfield, new 40/- without bayonet."²⁰⁵

W.A. is known to have purchased 1000 Magazine Lee-Speed rifles in 1900. All specimens of these rifles noted were made by the Birmingham Small Arms company. These arms were issued to the Volunteers in W.A. only, and thus survived through to 1904 when they were recorded in the Dominion Returns as still numbering 1000. From 1901 onwards arms purchases were a Commonwealth responsibility.

The arms of the early Cadet Corps 1883 - 1888 were few in number and were limited to shortened Enfields and short Snider rifles. In 1889 the Morris tubes were issued which allowed the use of



Figure 40 A Western Australian Contingent to the Boer War embarking with their Martini-Metford Mark I rifles at Fremantle wharf. These arms, and the Martini-Enfields, went to South Africa and possibly never returned (Photo courtesy of Battye Library. 5272P).

existing volunteer arms for target practice. It is evident however that the shortened rifles were still used for rifle drill.

The Cadet Force was established in 1897 and it is known that dummy rifles and Martini-Enfield carbines were repeatedly sought for them between 1896 – 1899. As far as is known only the dummy rifles were ever forthcoming. The Cadet Force does not appear to have been armed until 1903 – 1904 when two lots of Francotte Martinis, the miniature cadet rifle of .297/230 inch calibre were procured. They appear to have arrived in two lots, 1000 in 1903 and another 500 in 1904. The first order included a lot of 500 miniature socket bayonets. These arms were paid for by the W.A. Education Department. These little rifles are known to have been put on sale to the public in 1935. They were sold by Shimensons of Perth.²⁰⁶ The later Martini Cadet rifles used in W.A. appear from their butt marks to have originated in 1908 – 1909 and were Commonwealth arms, slightly heavier in weight and of a larger .310 inch calibre. The cadets were possibly issued Martini-Enfields and Magazine Lee-Enfields in the Commonwealth period but none have been noted with Cadet marks.

REVIEW OF MARKING

From the archives and the arms themselves a reasonable assessment of the marking of Colonial arms has been constructed. With the exception of the earliest Imperial arms, most markings are now known. The lack of certainty regarding the marking of some groups of the arms of this study is due in large part to the scarcity of surviving colonial arms upon which observations can be made.

The first recorded marking of W.A. arms were the Pattern 1853 Enfields of the W.A. Enrolled (Pensioner) Force issued c.1860. These Enfields were engraved (possibly prior to shipment) "W A over E F over number" on the buttplate and are believed to have stand numbers from 1 – c.300. They were followed by Snider-Enfield Mark II** conversions in 1870 which were also engraved "W A over E F over number" on their buttplates and had their own series of stand numbers beginning again at 1 through to 250. Short rifles for sergeants are also recorded as being on issue to the pensioners but none have been noted as yet. No other arms are known marked to this force.

From the earliest days of the volunteer movement, the careful marking of arms and recording of their issue was undertaken. The arms were marked according to regulations published by the War Office in London in 1862. There is no doubt that the first 200 Pattern 1853 Enfields received here in August 1862 were engraved by two unknown convicts in accordance with these regulations. No marks have as yet been noted on

Enfields but their marks, according to the regulation were "V over WA over number". These Enfields were augmented by a number of Enfields released from the Enrolled Pensioners in 1870. The Pensioner Force arms, as far as is known were not re-marked, it being thought forbidden to alter Imperial arms on loan. No re-marked specimen has been observed. Only one Enfield is known by its stand number. This was Enfield number 234 issued to the unfortunate Private Elsegood of the Perth Volunteer Rifles. This high stand number, 234, indicates that Enfields, additional to the 200 sent out in 1862 were acquired. As this rifle was the subject of discussion in 1872, two years after the Enrolled Force released a quantity of their estimated 300 Enfields to the volunteers, this may well have been an E.P.F. number.

The next lot of arms, the Deane, Adams revolver-carbines of 1864 intended for the Pinjarrah Mounted Volunteers were marked by C. Reichberg, a convict, in an unusual manner, partly the incorrect "W.A.V." requested by the Commandant and partly the "V over W A M" stipulated in the War Office regulations. The result was the unique "hybrid" mark "W.A.P.M.V. No.". The marking, (if done), of their 20 Smith and Wesson No. 2 Army revolvers of 1877 is unrecorded and no specimens are known.

The Volunteers were next issued with Snider long and short rifles, Mark III in 1877. These were received in two shipments and are definitely known to have been marked in the regulation manner, being engraved "V over W A over number" by prisoner Davis, also a convict. It is unknown how (or if), 50 Snider rifles procured in 1879 for the Albany Rifle Volunteers were marked, and the marks of 25 Pattern 1858 Snider Naval rifles procured in 1879 for the Fremantle Naval Artillery Volunteers are also unknown. "30 Revolvers" were procured for the Wellington Mounted Volunteers in December 1878 but like the Smith & Wessons of the Pinjarrah corps none are known to have survived and no reference to their type or marking was found. As mentioned in the text there is a notation in the records referring to "marking arms" for the Geraldton Rifle Volunteers in 1878. The details of these markings are unknown but it is thought the arms referred to were the new arms included in a mixed lot of new issue Sniders and E.P.F. Snider-Enfields sent to them in that year. It can be seen from the discussion then that the volunteers were issued, respectively, with a mixture of Volunteer and E.P.F. Enfields, followed by a mixture of Volunteer and E.P.F. Sniders. Volunteer arms were marked with volunteer marks while E.P.F. marks were left with E.P.F. marks.

Martini-Henry rifles were purchased in 1874 and again between 1881 – 1887 until virtually the entire corps was armed with them. A Martini-Henry was

noted bearing the initials of the Albany Defence Rifles. The initials were branded or deeply cut onto the left side of the butt. The initials are "A D R over number". Another two Martini-Henrys have been noted as being marked on the left side of the butt "M R V over number" and on the opposite side with the stand number repeated. These markings open up the possibility that other Martini-Henry arms also were marked to individual corps. If this individual marking by corps was widespread, then there must still be a considerable number of identification markings waiting to be recorded by arms researchers. Another mark noted on the Martini-Henrys are the initials "W.A.D.F." within a circle. These are the initials of the W.A. Defence Force and are thought to have been applied in or after 1893, when the Defence Force came into being. The Martini-Henrys are known to total at least 574, and stand numbers noted on the W.A.D.F. marked arms, 521 and 529, support this figure, but in doing so another question is raised. It has been seen that Martini-Henrys were issued throughout the Force generally, with some corps marking their own arms. From the specimens examined it is apparent that some individual corps each numbered their particular stand of arms from one upwards. The Albany Defence Rifles and the Metropolitan Rifle Volunteers totalled about 200 men at the time the Martini-Henrys were issued, indicating 200 rifles, therefore it is difficult to see how the W.A.D.F. marked Martini-Henrys, noted to have stand numbers in the 520s, could bear such numbers if they also began at one. From these three groups of stand numbers it would be possible to identify stands of Martini-Henrys totalling in excess of 700, which is contrary to the annual Returns total found of 574. It is clear therefore that the marks and numbers of the Martini-Henry group of arms is not as yet entirely clarified.

The commencement of the procurement program of .303 inch small-bore Martini arms began in 1895 with the issue of 700 Martini-Metford Mark I W.A. Pattern rifles, at which time the simplified ownership mark "W A over number" was adopted. This mark was applied to the wood of the right side of the butt of all arms with individual letter and numeral punches. The "W A" was separated from the numerals below them by a thin horizontal line which was never used on any other W.A. colonial arm. The Martini-Metford Mark Is were marked "W A 1-700". The Mark IIs which followed in 1897-98 are believed to have followed the practice of numbering all arms by "type" or "make", thus the 200 Mark IIs are thought to number "W A 701-900". No specimen of the Mark II has been found and most, if not all, are known to have gone to South Africa with the Third and Fourth Boer War Contingents. (See Trotter⁷⁶ pp.

303, 312). The .303 inch rifle procurement program continued with the receipt of 900 Martini-Enfield Marks I (and II?), W.A. Pattern rifles in 1898. A small lot of these arms were immediately issued to the Geraldton Rifle Volunteers and the W.A. Artillery at Albany. The marks of the Geraldton issue arms are thought to have been "WA over number" (possibly with a "D" suffix), while the Albany issue arms are known to have been marked "W.A.A. over number". The remainder of the Martini-Enfields were marked "WA over number over D" and seem to have been issued exclusively to the W.A. Mounted Infantry Contingents to the Boer War, between 1899 - 1901. These arms were augmented by further purchases of 200 in 1900 and 50 in 1901. The total number of M-Es purchased was 1150 and the stand number range noted (20 D, 40 D, 750 D, 783 D, 806 D, 1043 D and 1057 D) indicates that about 1100 of these had the "D" suffix. A small quantity of M-Es have been noted without the "D" suffix, (stand numbers 23 and 34), suggesting around 50 arms. Both of these arms are Mark IIs dated 1900, suggesting that they may have been the last 50 received in late 1901, and therefore possibly not issued to the W.A.M.I. It is thought that the "D" suffix is linked to the W.A.M.I. only.

It can be discerned from the illustrations that the style of letter punch used in the marking of the letters "W A" on the .303 inch Martini butts varied, although in most cases it remains constant within the "type" lot being marked, especially the Martini-Metfords. The location of these letters and numerals however often varies from butt to butt within the "type" group, suggesting idiosyncratic differences between workmen. The method used was the stamping of the letters and numerals with individual punches. Within the Martini-Enfield group the predominating style of letter and numeral punches and their location on the butt is typified by that shown in Figure 15. The style and size of letter and numeral punches used within this group does vary however and this variation is typified by Figure 26.

At this time at least c.251 -284 old W.A. Defence Force Martini-Henrys were converted in Perth to become Martini-Enfield Mark I W.A. Pattern rifles. These rifles were undoubtedly converted by a gunsmith named William Needham, using parts supplied from England. He was "Armourer to the Forces" from 1893. These W.A.D.F. Martini-Henry rifles were not re-marked when they were converted, as those noted have retained their old W.A.D.F. stamp and stand number unaltered.

During this period, 1000 Magazine Lee-Speed rifles were received. They were marked on the butt "WA over number", with stand numbers from 1-1000. They were issued exclusively to the local forces, none going to the contingents. These rifles were all marked with individual letter and

numeral punches. At least one specimen (Figure 14), has been noted as being marked with different style "W" and "A" punches. The practice of using individual letter punches ended with the colonial period. All subsequent marking, beginning around 1903-04, employed multi-letter die punches and included the circular Commonwealth die stamp. The W.A. Cadet Force mark "W A C F", found marked on the butts of Francotte Martinis is quite regular and uniform in the spacing of the letters, suggesting the possibility of a large die stamp, possibly in two parts, "W A" and "C F".

It can be seen from the foregoing discussion that a potentially serious anomaly arises in the marking of W.A. arms. It is apparent that as each "type" group of arms arrived from England they were marked with the appropriate letters and then marked with stand numbers beginning with one upwards. This practice was mentioned quite early by the regulations of 1862 and by Lt. Col. Harvest in his 1877 letter, where he recommended the numbering of the new Metropolitan Rifle Volunteer Sniders from "1 throughout". At times the volunteers were armed simultaneously with Volunteer and E.P.F. marked Enfields and Sniders, each lot respectively marked from one upwards. The result was pairs of Enfields, with each pair marked respectively, one, two, three etc, etc, and pairs of Sniders, each marked one, two, three and so on. It is not known with certainty how the early quartermasters maintained their issue records in the face of the potential problems this duplication presented but it is thought that each type of mark was recorded in separate registers and in the case of the Sniders the letter "P" found on the butt was possibly used to identify those arms issued to the Perth company of the W.A. Volunteers from those issued to any other volunteer company such as the Albany Rifle Volunteers or the Fremantle Naval Artillery Volunteers, who also had Sniders, it may also mean "Purchase". It must be borne in mind also, that by the time the volunteers were fully issued with Sniders, the Enfields were being withdrawn from service thus reducing the chance of duplication. In the case of those Sniders bearing the Enrolled Pensioner Force marks "W.A.E.F" it is thought that they were probably recorded as such when issued to the volunteers, thus avoiding confusion. By ensuring that no corps was issued with two lots of arms bearing the same numbers the potential for confusion would have been further reduced. In fact it has been noted that over the years particular care was taken to differentiate between different lots of arms, even to the extent of noting in the records of certain corps that they were issued with "converted Enfields" (ie. Snider - Enfields), rather than "Sniders". The Volunteers are known from records to have only purchased Snider Mark III rifles (Appendix 1), an entirely

new-made arm, while the E.P.F. is known from surviving specimens to have only had Snider-Enfield Mark II** conversions. The careful noting of these different types indicates that the "converted Enfields" were the former E.P.F. arms on loan from the Imperial government while the Sniders were the Colonial government purchased arms. It is also highly probable that this precise "type" recording of arms extended to their numbers as well. An example of this is the number on Private Elsegood's "lost or mislaid" Enfield of 1872. Elsegood's corps, the disbanded Metropolitan Volunteer Rifles had about 100 members armed with 100 Enfield rifles received per the *Bride* in 1862. These rifles were marked "V over W A 1 - 100", yet ten years later Elsegood's rifle is reported to bear number "234". The probable reason for this is that the corps numbers had risen above 100 by 1872 and E.P.F. Enfields had been issued to make up the difference. The E.P.F. Enfields became available in 1870 when the E.P.F. received their new Snider Enfields.

The Martini-Henrys are known to have been marked to a variety of individual corps, and to the W.A.D.F. itself. With so few known to have survived it is difficult to be certain about their marks and numbers, but it appears that, like the Enfields and Sniders, they also had parallel sets of stand numbers, all beginning at one. The potential problems arising from this practise of stand number duplication within a single "type" of arm are self evident, and must have required constant vigilance on the part of the ordnance storekeeper during the re-allocation of arms between corps, as occurred with some frequency between 1885 - 1895.

In later years, as each shipment of the different types of .303 inch arms arrived they were marked "W A over 1 upwards, throughout the number of their particular lot. Thus by 1900 W.A. had separate lots of .303 inch Martini-Metfords, Martini-Enfields and Magazine Lee-Speeds, with each lot marked respectively "W A over 1, 2, 3 etc. throughout. Marking arms by "type" in lots could again potentially lead to administrative confusion as in the case of the earlier arms as having three .303 inch calibre rifles marked "WA over 1", three "WA over 2", three "WA over 3" etc., makes it difficult to control the issue or recall of arms. Again, the careful notations in the Returns over the years showing that the various corps were issued with named lots of arms, either Martini-Henrys, Martini-Metfords, Martini-Enfields or Lee-Speeds indicates separate "type" recording in either separate registers, or separate sections of a larger register.

One last volunteer arm, residing in the W.A. Museum collection (AMD 150), which must be described, is a Pattern 1853 Enfield long rifle, third

model. This arm deserves a mention as it is engraved on the butt plate tang "V" over the stamped number "96". It is possible that this plain "V" code is an arms identification code from an eastern colony, but it may also be a simplified W.A. volunteer code, possibly even the mark of the 200 Enfields shipped on the *Bride* in 1862. If this mark is indeed on one of the *Bride* arms, then it does not conform strictly to the regulations of 1862 as referred to by Col. Harvest when he discussed the marking of arms in his letter of October 1864. If from W.A., the mark has not appeared with any clarity in the archival record and therefore must await verification, but it cannot be dismissed out of hand.

CONCLUSION

Following Wieck and Grant, all corps and their issue long arms with their markings have been investigated and the results presented. As stated, the lack of surviving arms specimens is the greatest single obstacle preventing a more comprehensive detailing of these subjects. It is felt however that all major groups of arms have been examined and described. Some small shipments of "arms" or "pistols" were noted but as they were not identified specifically they could have been intended equally for the Police or Convict Establishment rather than the Volunteers, consequently they were not included. Side arms for the upper ranks of the corps, with the exception of two Webley revolvers ordered for the Permanent Force in 1893, are invariably referred to as "revolvers". Officers generally purchased their own pistols, leaving no record of type. These arms therefore have of necessity been excluded from this paper. It is felt however that numbers of these small lots found in the records described simply as "arms" could actually have been procured to "top up" the arms stands of the various corps as needed, when enrolments rose. The important groups of arms and their quantities however are given with confidence. There were c.500 Volunteer and Enrolled Pensioner Force Pattern 1853 Enfields and c.470 Volunteer Sniders and E.P.F. Snider-Enfields. There were at least 574 Martini-Henrys, 900 Martini-Metfords, 1150 Martini-Enfields, and at least c.251 – 284 Unofficial Conversions of W.A. Martini-Henry rifles into Martini-Enfields. Also there were 1000 Magazine Lee-Speeds, W.A.'s first modern repeating military rifle, together with the 1500 early post Federation Francotte Martini cadet rifles.

It must be said that despite statements to the contrary by previous writers, no evidence of the issue of carbines to the artillery corps was found. Instead, where their arms were mentioned, they

were described as being conventional long arms, Naval short rifles, or Sniders on loan, only the Permanent Force of 1893 being documented as having Martini-Henry carbines. The early mounted corps were also found to have revolvers or revolver-carbines only, with conventional long arms being on issue for target practice. The later mounted infantry were armed with infantry long arms, such as Sniders, and later the various .303 inch Martini arms.

The "recycling" of arms between various corps illustrates a certain practical frugality in government defence expenditure, and certainly illustrates the problems arising from these constant exchanges for the quartermasters and armourers who had to keep track of arms issues by means of stand registers.

It can be seen that arms were marked from the earliest days. The E.P.F. arms were possibly engraved with their marks prior to shipment to W.A. Between 1862 – 1878, all volunteer arms marking seems to have been performed by convicts while for a time after that date it appears to have been contracted out, not always with entirely satisfactory results, as a letter from Lt. Col. Harvest to the Colonial Secretary in 1878 shows. In discussing the quality of free, compared with convict labour workmanship, he states:

"I find that Tradesmen in Prison work their best with the view of obtaining a reduction of Imprisonment – Last year I had an Engraver from the Prison at Fremantle lodged in the Perth Gaol, marched to Perth Barracks daily to engrave Volunteer Rifles under my supervision. He worked very well and in consequence was let off the remainder of his sentence, nearly expired – Some months afterwards more Rifles required engraving and I was forced to employ the same man out of prison – his charge was high and the work not so satisfactorily performed".²⁰⁷

Harvest was referring to Convict Davis and the 118 long and short Snider rifles of early 1877. The second lot requiring engraving were the 33 Sniders of mid 1877. Between 1878 and 1893 little is known regarding the marking of arms. From the Martini-Henry specimens it appears that at least on two occasions a corps marked its own arms, and judging from the individual corps names etched on surviving sword blades of this period, it may be more widespread a practise than presently thought. Also during this time many quartermaster duties were apparently done within the volunteers with some duties devolving upon a Corporal Rush, who cleaned, repaired and generally seems to have issued and shipped arms to the new corps and outlying stations.²⁰⁸ From 1893 until Federation, William Needham, the "Armourer to the Forces" took charge of the care of arms. It may have been Needham who introduced the "W A D F" stamp into the service. Due to the variations encountered in the styles and locations of the butt marks and

numbers of the .303 inch Martinis, it is believed that in some cases at least, these arms were marked by different people, possibly at different locations. It is believed Mr. Needham may have been engaged to number and mark some batches of .303 inch calibre Martinis between 1895 and 1901, when the Commonwealth took over.

It is acknowledged that certain small discrepancies appear in the quantities of arms listed and inconsistencies exist in the archival record. The means of eliminating these anomalies is believed to exist. It was noted by Lt. Col. Harvest in a Minute to the Colonial Secretary in 1878 that, "Every item of Volunteers expenditure passes thro' my hands and is noted in a book in my office".²⁰⁹ Until a researcher is fortunate enough to locate Colonel Harvest's (and his successor's), book and the arms registers, the anomalies in the story of Colonial military arms will remain. It is hoped that in the absence of such records, this present paper will form a solid basis for further research.

ACKNOWLEDGEMENTS

The author would like to acknowledge James Grant for his assistance and advice on the Volunteer Corps; Ron Cook, for his helpful criticisms on the arms themselves. Nathan Thompson, Sgt. R. Warburton (W.A. Police), Margaret Needham, Elizabeth Mansom and the Battye library staff are also thanked, as are those institutions and individuals who allowed me access to arms and records in their care.

¹ Dennison, W., *A Short History of the 63rd of Foot in Western Australia 1829 – 1833*, Privately Published, Perth, (n.d.), p. 9.

² Priest, G., *The Brown Bess Bayonet 1720 – 1860*, Tharston Press, Norwich (U.K.), 1986, pp. 102, 133, 156. According to R.J. Wilkinson Latham, *British Military Bayonets 1700 – 1945*, Hutchinson, London, 1967, p. 77, extra service arms and arms issued on loan for temporary purposes did not receive a corps mark, unless issued for active service. They only had the mark of the issuing depot.

³ Skennerton, I.D., *Australian Service Longarms*, Privately Published, QLD., 1976, pp. 68–99 and Halls, C., *Guns in Australia*, Hamlyn, Sydney, 1974, pp. 69–70.

⁴ Skennerton, I.D., *A Treatise on the Snider*, Privately published, Qld., 1977, p. 163.

⁵ Broomhall, F.H., *The Veterans*, Hesperian Press, Perth, 1990 p. 2.

⁶ Battye Library, CO 18/93, quoted in Broomhall, p. 2.

⁷ *Op cit.*, Broomhall, pp. 29, 48.

⁸ Battye Library, Acc. 36 513/229, 22nd May 1857. These carbines are mentioned again in a letter (Acc. 36 509/339), to the Colonial Secretary from members of the Swan Volunteer Rifle Corps which unsuccessfully attempted to acquire arms in 1861. The letter, dated October 29 requests the supply of "20 carbines, bayonets and accessories belonging to the Police Force to be issued to the Swan Rifles for drill purposes, providing they can be spared." The police reply of the 1st of November states "twenty carbines can be spared but the swords belonging to them are all served out to the men at the stations...the carbines are all double breasted (sic) ones". Technical information on these carbines may be found in Skennerton's *Australian Service Longarms* pp. 12 and 76 and Blackmore, H.L., *British Military Firearms 1650 – 1850*, Jenkins, London, 1969, pp. 219–220.

⁹ Battye Library, Votes and Proceedings of W.A. Parliament, 1876, Governors Despatch No. 25, enclosure Number 1, 18/2/76.

¹⁰ *Op cit.*, Skennerton, *A Treatise on the Snider*, p. 107.

¹¹ *Op cit.*, Broomhall, p.58. In 1868 there were 190 men under arms on a daily basis in the metropolitan area. 65 men in the outstations remained armed with smoothbore muskets. Purdon, C.J., *The Snider-Enfield Rifle*, Historic Arms Series No. 24, Museum Restoration Services, New York & Ontario, 1990, p. 31. Quoting from a British "Schedule of Correspondence, compiled 1867—", the number of "Sniders" for Perth W.A. is given as 135 long, 15 short in 1870.

¹² Battye Library, Acc. 36 805/14. Commandants letter, 26th November 1875, "The Enfields now on loan were spare in the colony owing to the Pensioner Force being armed with Sniders".

¹³ Battye Library, Acc. 144, 3rd January 1881. 67 outstation arms plus 7 others were auctioned by Lionel Samson.

¹⁴ Battye Library, Acc. 144, 15th December 1880. Returns of stores of the disbanded E.P.F. The stores official reported that the E.P.F. "Never had the Martini-Henry Rifle". Photographs in Broomhall show the final parade of the Enrolled Guard in 1887, all are still armed with Snider-Enfields.

¹⁵ Battye Library, Acc. 49, Vol. 43, letter 1443. Acc. 36 509/335. The issue of these Colonial muskets was approved on 30th September 1861.

¹⁶ Battye Library, Newspaper Archives. *Perth Gazette*, 12th September 1862 indicates that the rifles arrived on the *Bride* on 16th July 1862, replacing "Brown Bess" muskets. These arms were requested by the Executive Council on the 20th August 1861. (Acc. 1058, Vol. 1858-1866, p. 147).

¹⁷ Battye Library, Acc. 36 496/9, 9th August 1862

¹⁸ Battye Library, Acc. 36 496/9, 9th August 1862. A "stand" is the military term for a group of arms issued to a corps and the identifying number put on the arm becomes the stand number by which it is known. The term also refers to the various accoutrements which accompany each firearm, these accoutrements also bear the stand number of the arm.

¹⁹ Battye Library, Acc. 49 Vol. 44, Letter 519, 12th August 1862.

²⁰ State Records, South Australia, supplied by A.F. Harris, private correspondence, 9th February 1994.

²¹ Battye Library, Acc. 36 548/361, 5th October 1864.

²² Battye Library, Acc. 36 856/331, 5th July 1872, 29th November 1872.

²³ Wieck, G., *The Volunteer Movement in Western Australia 1861 – 1903*, Paterson Brokensha, Perth (n.d.) p. 29.

²⁴ *ibid*, Wieck, p. 29.

²⁵ Battye Library, Newspaper Archives, *Perth Gazette*, 25th July 1862.

²⁶ *Op. cit.*, Wieck p. 30.

²⁷ Battye Library, Acc 36 548/361, CSO correspondence. The Enfield Rifles referred to are the 200 per the *Bride* in 1862.

²⁸ Battye Library, Acc. 36 548/361. Biographical details of this convict will be found in Erickson, R., *Dictionary of Western Australians. Bond 1850 – 1868*, University of Western Australia Press, Perth, 1979, p. 447.

²⁹ Battye Library, Acc. 36 805/10. Research revealed a letter dated 29th October 1873 which indicates that the 12 swords were ordered that year, (Acc. 36 759/170). They were 12 Light Cavalry Swords, Staff Sergeants Pattern with bags and knots received from Wilkinsons, per the *Ivy* on 6th May 1874, for Pinjarrah Mounted Volunteers (Acc. 36 764 pp. 48–51).

³⁰ Battye Library, Acc. 36 805/12. The convict ship name is probably *Hougoumont*. Fawcett appears mistaken in both the date of issue and the origin of these arms. They were procured especially for him, direct from England in 1864. This correspondence is possibly the source of Wieck's statement that the P.M.V. was originally armed from the guard of a convict ship.

³¹ Battye Library, Acc. 36 805/14.

³² Battye Library, Acc. 36 847/219.

³³ Battye Library, Acc. 36 847/248. V.R. Blakemore, Charlotte Street, Birmingham.

³⁴ Jinks, R.G., *History of Smith & Wesson*, Beinfeld, Hollywood, 1977, pp. 50 – 52, 105 – 108, and Neal, R.J. & Jinks, R.G., *Smith & Wesson 1857 – 1945*, Barnes/Yoseloff, N.Y. & London, 1975, pp. 62 – 65, 106 – 111. Mr Jinks opined that in his view he felt it more likely that the revolvers supplied would have been the .38 calibre arms. Letter to author, 18.3.1994.

³⁵ Battye Library, Acc. 36 CSR 899/198.

- ³⁶ Battye Library, Acc. 36 CSR 899/195.
- ³⁷ Battye Library, W.A. Yearbook, Military Returns 1880 – 1882.
- ³⁸ Battye Library, Acc. 36 729, 24th May 1870.
- ³⁹ *Op cit.*, Halls, p. 140.
- ⁴⁰ Battye Library, Acc. 527/1579.
- ⁴¹ Battye Library, Acc. 36 708/213. According to Temple, B.A., and Skennerton I.D., *A Treatise on the British Military Martini 1869 – 1900*, Vol. 1. Privately Published, Queensland, 1983, p. 127, Martini-Henry carbines were not produced until 1877.
- ⁴² Battye Library, Acc. 36 764/65.
- ⁴³ *Op. cit.*, Wieck, p. 36 and Grant, J.R. *From Captains to Colonels*, Burrigge, Perth, 1991 pp. 12, 52, 53 – 59.
- ⁴⁴ Battye Library, Acc. 390/47, Vol. 1, 20th May 1874, Confidential Despatches.
- ⁴⁵ Battye Library, Acc. 144, 25th November 1880.
- ⁴⁶ Battye Library, Votes and Proceedings of W.A. Parliament 1882. Report on the Volunteer Force 1881–82.
- ⁴⁷ Battye Library, Acc. 527/321, Minute Paper, 15th January 1884. This document indicates that the corps still lacked arms at this date.
- ⁴⁸ Battye Library, Newspaper Archives, *West Australian*, 13th May, 1887.
- ⁴⁹ Battye Library, Acc. 36 638/170. As already mentioned it appears that at least 40 of the men on the roll of the Pinjarrah corps were without equipment and uniform. They may also have been deficient in arms.
- ⁵⁰ Battye Library, Acc. 36 705/121.
- ⁵¹ Battye Library, Acc. 36 705/17.
- ⁵² Battye Library, Acc. 36 728/297.
- ⁵³ Battye Library, Acc. 36 728/301.
- ⁵⁴ Battye Library, Acc. 36 728/292.
- ⁵⁵ Battye Library, Acc. 36 805/14.
- ⁵⁶ Battye Library, W.A. Yearbook. Military Returns 1874.
- ⁵⁷ Battye Library, Acc. 36 805/14. These loan Enfields consist of a portion of the gift Enfields which arrived in the *Bride* in 1862 and others lent from the E.P.F. stores, ie. "on loan" from the Imperial Government.
- ⁵⁸ Battye Library, W.A. Yearbook. Military Returns 1875.
- ⁵⁹ Battye Library, Acc. 36 822/26, 27. The Pattern 1860 actually refers to the pattern of an earlier short rifle adopted in 1860. These 1877 short rifles were virtually identical, except were new made arms rather than conversions of Enfields.
- ⁶⁰ Battye Library, Acc. 36 847/219, 243, 244, 246, 248. Vol. 899/206, 221, 222, 223, 225, 226. Vol. 822/26, 27.
- ⁶¹ Battye Library, Acc. 36 847/248, 249, 250.
- ⁶² Battye Library, Acc. 36 856/1–4.
- ⁶³ Battye Library, Votes and Proceedings of W.A. Parliament, 1877/78. Expenditure of Annual Grant to Volunteers. Rifles supplied by Crown Agent per *Eulie* charged to Metropolitan Rifle Volunteer account.
- ⁶⁴ Battye Library, Acc. 36 847/248, 249, 250.
- ⁶⁵ Battye Library, Acc. 36 899/221, 222.
- ⁶⁶ Battye Library, Acc. 36 899/204. The sound rifles referred to were those not damaged in transit by sea water.
- ⁶⁷ Battye Library, Acc. 36 899/231. Biographical details of a convict thought to be this man will be found in Ericson, R., *Dictionary of Western Australians. Bond 1850 – 1868*. University of W.A. Press, Perth, 1979, p. 139.
- ⁶⁸ Battye Library, W.A. Yearbook. Military Returns 1881.
- ⁶⁹ Battye Library, Acc. 527 243/12. Letter, 19th November 1878.
- ⁷⁰ Battye Library, Acc. 527/321. Minute, 15th January 1884. Stores in charge of Volunteers Department.
- ⁷¹ Battye Library, W.A. Yearbook, Returns of Land Forces to 31st December 1884.
- ⁷² Battye Library, Acc. 527/1531/35.
- ⁷³ Battye Library, Votes and Proceedings of W.A. Parliament 1887. Commandants Report 31st December 1886.
- ⁷⁴ From a private collection in Bunbury. The butt and body of the first rifle are both marked as Mark II, but are made by different manufacturers. The body, by London Small Arms Co. is dated 1880, while the Enfield made stock is dated 1883. This rifle could be from an 1885 order for 101 Mark II Martini-Henrys. The butt and body of the second rifle are both manufactured by Enfield. The butt retains its correct checkered buttplate. Because of the poor condition of the butt, the stand number could also be "3".
- ⁷⁵ Battye Library, W.A. Statistical Register. Naval and Military Returns 1895.
- ⁷⁶ Trotter, G.B. (1993). The Martini-Enfield Rifle in Western Australia. *Rec. West. Aust. Mus.* 16 (3) p. 298.
- ⁷⁷ Battye Library, Newspaper Archives, *The Australian Advertiser*. 19th August 1895.
- ⁷⁸ *ibid*, Trotter, pp. 298, 299, 305. This paper describes the purchase of the Martini-Metfords Mark I and II and the Magazine Lee-Speeds.
- ⁷⁹ Battye Library, Acc. 36 759/162.
- ⁸⁰ Battye Library, Acc. 36 759/62. A letter dated 1st October 1872 (Acc. 36 708/209) states the number of smoothbores to be "twenty, for drill".
- ⁸¹ Battye Library, Votes and Proceedings of W.A. Parliament 1876. Governors Despatch No. 25. Inclusion Number 2. 18th February 1876.
- ⁸² Battye Library, Acc. 36 788/115.
- ⁸³ Battye Library, W.A. Yearbook. Military Returns 1875.
- ⁸⁴ Battye Library, Newspaper Archives, *Inquirer* 12th May 1875. These Sniders could only have been borrowed from the E.P.F.
- ⁸⁵ Temple, B.A., and Skennerton, I.D., *A Treatise on British Military Martini 1869 – 1900*, Vol. 1, Privately Published, Queensland, 1983, p. 85.
- ⁸⁶ Battye Library, Acc. 36 847/249, and Votes and Proceedings of W.A. Parliament 1876. Governors Despatch No. 25. Inclusion Number 1 & 2.
- ⁸⁷ Battye Library, Acc. 144, 13th April 1881.
- ⁸⁸ Battye Library, Acc. 144, 10th May 1881.
- ⁸⁹ Battye Library, Votes and Proceedings W.A. Parliament 1882, Commandants Report, 1881. The Commandant reported an expenditure of 225 pounds for Arms and Ammunition purchased from the War Department for the Fremantle Rifle Volunteers, the Naval Artillery Volunteers and ammunition for the service generally. Another record shows that three chests and one case of rifles "for the Volunteer Forces" arrived per the *Daylight* in that year. These chests are believed to include the 28 M-H rifles for the F.R.V. and unknown other items. They were ordered on 16th October 1880. (Acc. 527/1326)
- ⁹⁰ Battye Library, Acc. 527/321 1884
- ⁹¹ Battye Library, Votes and Proceedings W.A. Parliament, 1887. Commandants Report 1886 – 87.
- ⁹² Battye Library, Acc. 527/2893/87.
- ⁹³ Battye Library, W.A. Statistical Register. Naval and Military Returns 1895 – 1900.
- ⁹⁴ *Op. cit.*, Wieck, pp. 39, 40.
- ⁹⁵ Battye Library, Acc. 36 805/14
- ⁹⁶ Battye Library, W.A. Yearbook. Military Returns 1875 – 1878.
- ⁹⁷ Battye Library, Acc. 36 900/331.
- ⁹⁸ Battye Library, Acc. 527/321
- ⁹⁹ Battye Library, W.A. Yearbook. Military Returns 1878 – 1886.
- ¹⁰⁰ Battye Library, Votes and Proceedings of W.A. Parliament 1886 – 1888. Commandants Reports 1886–87, 1887–88.
- ¹⁰¹ Battye Library, Votes and Proceedings of W.A. Parliament 1887–88.
- ¹⁰² Battye Library, W.A. Yearbooks 1893–94 Military Returns, and W.A. Statistical Registers 1895 – 1900. Naval and Military Returns.
- ¹⁰³ *Op cit.*, Grant, p. 43. Grant states 1878. The Returns for 1877 show the G.R.V. with 53 men.
- ¹⁰⁴ *Op cit.*, Wieck, p. 42.
- ¹⁰⁵ Battye Library, Votes and Proceedings of W.A. Parliament 1879 Expenditure of Annual Grant to Volunteers 1877–78.
- ¹⁰⁶ Battye Library, W.A. Yearbook, Military Returns 1880.
- ¹⁰⁷ Battye Library, Acc. 527/321.
- ¹⁰⁸ Battye Library, Votes and Proceedings of W.A. Parliament 1887 Commandants Report 1886.
- ¹⁰⁹ Battye Library, W.A. Statistical Register, Naval and Military Returns 1896 – 1898.
- ¹¹⁰ *Op. cit.*, Trotter, pp. 285 – 314. (Halls, p. 142 states M-E Mark II).
- ¹¹¹ Battye Library, Votes and Proceedings of W.A. Parliament 1884 Commandants Report 1883. Votes and Proceedings W.A. Parliament 1888. Commandants Report 1887.
- ¹¹² Battye Library, Votes and Proceedings of W.A. Parliament 1878 Expenditure of Annual Grant to Volunteers 1878.

- ¹¹² Battye Library, Newspaper Archives, *W.A. Times*, 31st December 1878.
- ¹¹³ *Op cit.*, Wieck, p. 43.
- ¹¹⁴ Battye Library, Votes and Proceedings of W.A. Parliament 1878. Expenditure of Annual Grant to Volunteers 1877–78.
- ¹¹⁵ Battye Library, Acc. 527/1531/18. These were probably the Enfield rifles used for target shooting. Volunteers received subsidised arms and ammunition to use to practice shooting. It was probably these arms they sought to retain.
- ¹¹⁶ Battye Library, Acc. 527/243/1.
- ¹¹⁷ Battye Library, Acc. 527/1144.
- ¹¹⁸ Battye Library, Newspaper Archive, *Albany Mail*, 1st April 1884, describes a shooting match by the A.R.V. where “The company are provided with converted Enfield rifles, but before next year will probably be furnished with Martini-Henri (sic) rifles”.
- ¹¹⁹ Battye Library, Votes and Proceedings of W.A. Parliament 1885 – 1887. Commandants Report 1884–85.
- ¹²⁰ Darling, A.D., *Red Coat and Brown Bess*, (Historical Arms Series 12), Museum Restoration Service, Canada, 1978, p.52.
- ¹²¹ Battye Library, Votes and Proceedings of W.A. Parliament 1887. Commandants Report 1886.
- ¹²² *Op cit.*, Wieck, p. 51.
- ¹²³ Battye Library, Votes and Proceedings of W.A. Parliament 1889–91. Commandants Report 1889.
- ¹²⁴ Battye Library, W.A. Yearbook. Military Returns 1891.
- ¹²⁵ Battye Library, W.A. Statistical Register. Naval and Military Returns 1896.
- ¹²⁶ Battye Library, W.A. Statistical Register. Naval and Military Returns 1900.
- ¹²⁷ Battye Library, Newspaper Archive, *Albany Advertiser*, 10th January 1901.
- ¹²⁸ *Op cit.*, Wieck, p. 45.
- ¹²⁹ Battye Library, Acc. 527/321.
- ¹³⁰ Battye Library, Votes and Proceedings of sW.A. Parliament 1884. Commandants Report 1883–84.
- ¹³¹ Battye Library, W.A. Yearbook, Naval and Military Returns 1893–94.
- ¹³² Battye Library, W.A. Statistical Register, Naval and Military Returns 1895 – 1900.
- ¹³³ *Op cit.*, Halls, p. 140.
- ¹³⁴ *Op cit.*, Skennerton, p. 96.
- ¹³⁵ Battye Library, Acc. 527/1144.
- ¹³⁶ Battye Library, Votes and Proceedings of W.A. Parliament 1882. Commandants Report 1881.
- ¹³⁷ Battye Library, Acc. 527/321. It was not possible to identify these percussion muskets from the records. It is possible that they were Pattern 1839 or 1842.
- ¹³⁸ Battye Library, Acc. 144, 12th May 1881.
- ¹³⁹ Battye Library, Votes and Proceedings of W.A. Parliament 1889. Commandants Report 1888.
- ¹⁴⁰ Battye Library, Newspaper Archives, *West Australian*, 2nd September 1891.
- ¹⁴¹ *Op cit.*, Halls, p. 140.
- ¹⁴² *Op cit.*, Skennerton, p. 120.
- ¹⁴³ *Op cit.*, Grant, p. 31. Grant says these rifles were issued in June.
- ¹⁴⁴ Battye Library, Newspaper Archive, *Australian Advertiser*, 8th May, 1895.
- ¹⁴⁵ Battye Library, W.A. Statistical Register. Naval and Military Returns 1896 – 1900.
- ¹⁴⁶ Battye Library, Votes and Proceedings of W.A. Parliament 1894. Commandants Report to June 1894.
- ¹⁴⁷ Battye Library, W.A. Statistical Register, Naval and Military Returns 1900.
- ¹⁴⁸ Battye Library, Newspaper Archive, *Australian Advertiser*, 28th August 1895.
- ¹⁴⁹ Skennerton, I.D., *The British Service Lee*, Privately Published, Qld., 1982. On page 56 of this publication are to be found a discussion on, and illustration of, this Metford barrel.
- ¹⁵⁰ Shannon, R.B., *Colonial Australian Gunsmiths*, Wentworth Press, Sydney, 1967, p.18. Biographical details supplied by Mrs Margaret Needham show that William Vernon Needham was born in London on 21st August 1851 and died in Perth in March 1928, aged 77 years. He retained his connection with the state government even after Federation, being Armourer to the Police at the time of his death. As well as being able to manufacture and repair firearms, it is probable that he imported arms into W.A. through J.V. Needham, the firearms company, of London and Birmingham, to whom he was related.
- ¹⁵¹ Battye Library, W.A. Almanack and Directory, (Stirling Bros.) 1887–1888. W.A. Directory. (H.Piersenne), p.15, 1894. W.A. Directory, (Wise's), p.183, 1895
- ¹⁵² Battye Library, W.A. Almanack and Directory, 1888, (Advertisement).
- ¹⁵³ Battye Library, Executive Council Minutes, 9th May 1893, 567/93.
- ¹⁵⁴ Battye Library, Acc. 527 CSO Letter received, 9th May 1893, 742/93.
- ¹⁵⁵ Battye Library, W.A. Statistical Register, Naval and Military Returns 1900.
- ¹⁵⁶ Battye Library, W.A. Statistical Register, Naval and Military Returns 1895, and, Dominion Returns for Land Forces to 31st December 1904, quoted in private correspondence by Skennerton and Temple 18.7.1991, 18.3.1992.
- ¹⁵⁷ Battye Library, W.A. Government Gazette 6th April 1893, p. 347.
- ¹⁵⁸ Public Records Office, South Australia. *The South Australian Military and Police Forces 1887*, Booklet, reprinted by Harris, A.F., Macgill, S.A. (n.d.)
- ¹⁵⁹ *Op cit.*, Trotter, p. 289.
- ¹⁶⁰ Battye Library, W.A. Government Gazette 6th April 1893, p. 347.
- ¹⁶¹ Battye Library, Acc. 527 840/93.
- ¹⁶² Battye Library, W.A. Statistical Register. Naval and Military Returns 1895, 1900.
- ¹⁶³ Murray, P.L., *Records of the Contingents to the War in South Africa 1899 – 1902*, Defence Department, Melbourne, 1911, p. 441.
- ¹⁶⁴ Votes and Proceedings of W.A. Parliament 1900. Commandants Report 1899.
- ¹⁶⁵ *Op cit.*, Trotter, p. 298.
- ¹⁶⁶ Battye Library, W.A. Statistical Register 1895. Naval and Military Returns.
- ¹⁶⁷ Battye Library, CO 18 W.A. 12, 1900. Agent Generals Report 1899.
- ¹⁶⁸ *Op cit.*, Trotter, pp. 311 – 313. Since this paper was published it has been determined that the Pattern 1876 bayonet would fit the Mark II without any alteration, the rifle foresight ramp only requiring a simple modification.
- ¹⁶⁹ *ibid*, pp. 298 – 307. The author presented documentary evidence to support the acquisition of 200 M-Es in 1898 and 200 more in 1900.
- ¹⁷⁰ *ibid*, pp. 298 – 307.
- ¹⁷¹ Public Records Office, London. “Issues of .303” Arms made to the Colonies since Introduction”, supplied by B.A. Temple in personal correspondence 11.7.1993.
- ¹⁷² Battye Library, Votes and Proceedings of W.A. Parliament, Commandants Report 1900. “Two hundred and nineteen rifles were sent to South Africa with the First and Second Contingents” (of 222 NCOs and men). A document concerning the handing in of Martini-Metfords in Cape Town for Magazine Lee-Enfields, 28th November 1899, exists in the Battye archives, (Document from the South African War, 827/7, p.29). In response to a survey of W.A. marked arms for a previous paper on the W.A. Pattern Martini-Enfield, one W.A. marked “Martini .303” was reported as returned to Australia from Lesotho, South Africa, by a Mr Jurgen Schultze of N.S.W. in c.1970.
- ¹⁷³ Battye Library, Votes and Proceedings of W.A. Parliament 1901, Commandants Report 1900 and W.A. Statistical Register, Naval and Military Returns 1900. The Report shows that there were 251 Martini-Henry rifles awaiting conversion at this time, while the Returns show that the Civil Service Corps mustered 284 men, now known to have been armed with Unofficial Conversions. This latter figure is also circumstantially supported by the Dominion Returns of 1904 which show that 287 M-Hs were lost from the original total of 574, almost the exact total of men in the Civil Service Corps.
- ¹⁷⁴ Battye Library, Newspaper Archives, *West Australian*, 13th February 1900.
- ¹⁷⁵ Battye Library, W.A. Statistical Register. Naval and Military Returns 1900.
- ¹⁷⁶ Public Records Office, London, “Issues of .303” Arms made to the Colonies since Introduction”. Quoted by B.A. Temple in private correspondence 11.7.1993.
- ¹⁷⁷ Army Museum of W.A. Archives, Army General Orders 1903 – 1909.

- 178 Skennerton I.D., *Australian Service Bayonets* Privately Published, Q.L.D. 1976, p.17. Dominion Returns, 1904, 620 Pattern 1903 bayonets were listed as on order for W.A. These are the accompanying bayonet for the SMLE Mk. I.
- 179 Batty Library, Votes and Proceedings of W.A. Parliament 1884, 1889. Commandants Report 1883, 1888.
- 180 Batty Library, Votes and Proceedings of W.A. Parliament 1889. Commandants Report 1888. These tubes were used by the recruits of the Perth, Fremantle, Guildford and Geraldton Corps.
- 181 Batty Library, Votes and Proceedings of W.A. Parliament 1897. Commandants Report 1896.
- 182 Batty Library, Newspaper Archives, *Albany Advertiser*, November 1895.
- 183 Batty Library, Votes and Proceedings of W.A. Parliament. Commandants Reports 1898 – 1900.
- 184 Treasury Department Archives, Reports of Public Accounts 1896 – 1902.
- 185 Jones, D., "Cadets and Military Drill" (Chap. 2) in Bessant R., and Maunders, D., (eds), *Mother State and Her Little Ones*, Centre for Youth and Community Studies, Melbourne, 1987. The cadet enrolment in 1898 was 155 Senior and 276 Junior.
- 186 Batty Library, Commonwealth Parliamentary Acts, "Cadet Force Australia 1903", adoption by Secondary School Senior Cadets of .303 M-E (single-loader), p. 3, and 1908, adoption by Senior cadets of M L-E, p.2.
- 187 Op cit., Purdon, p. 31 (see footnote 11).
- 188 Batty Library, Votes and Proceedings of W.A. Parliament 1882, Report.
- 189 Batty Library, Votes and Proceedings of W.A. Parliament 1882, Report.
- 190 Batty Library, W.A. Yearbook. Military Returns 1883 – 1884.
- 191 Batty Library, Votes and Proceedings of W.A. Parliament 1876. Despatch No. 25.
- 192 Batty Library, Votes and Proceedings of W.A. Parliament 1889. Commandants Report 1888.
- 193 Batty Library, Parliamentary Debates (Hansard), 1887, p. 227.
- 194 Batty Library, CO 18 210. Reel 1707, 1888.
- 195 Batty Library, W.A. Yearbook and Statistical Registers, Military Returns 1884 – 1895.
- 196 Batty Library, W.A. Yearbook 1893 – 1894. Military Returns.
- 197 Batty Library, Votes and Proceedings of W.A. Parliament 1882. Commandants Report 1881.
- 198 Batty Library, CSO 4123/1885, Minute paper 9th October 1885. "101 Rifles, B.L., M-H, Mk II, Short Butts". Votes and Proceedings of W.A. Parliament 1885–86. Commandants Report 31st December 1885. The 101 rifles may have been part of the larger order received in 1886.
- 199 Batty Library, Votes and Proceedings of W.A. Parliament 1887. Commandants Report 1886–87. This order may have included the order for 101 rifles of 1885.
- 200 Batty Library, Votes and Proceedings of W.A. Parliament 1887. Commandants Report 1887.
- 201 Batty Library, CO 18 218, Reel 2664, 1893.
- 202 Batty Library, CO 18 210, Reel 1707, 1888.
- 203 Batty Library, Votes and Proceedings of W.A. Parliament 1899. Commandants Report 1899.
- 204 The precise fate of the rifles accompanying the contingents is uncertain. The archival record allows for a number of possible explanations. The Dominion Returns of 1904 show that the 900 M-Ms were reduced by 272 to 628. The approximately 1434 M-Es, (1150 M-Es and c.284 Unofficial Conversions), were reduced by c.606 to 828. The total losses are therefore 272 plus c.606, or c.878, virtually the exact total of 872 NCOs and men of the six contingents. The M-Es however, could also have been removed from the Returns list due to General Order 263, of 16th Nov. 1903, which required the W.A. military authorities to allocate 600 M-Es to the rifle clubs. Unless firm evidence is located, this matter must remain inconclusive.
- 205 Army Museum Archives, General Orders 1903 – 1909. No Martini-Mefford rifles were offered for sale even though they were available.
- 206 Comments by two former owners of these rifles, related to author in 1990 and 1994.
- 207 Batty Library, Acc. 527/243/12, Letter 19th November 1878.
- 208 Batty Library, Votes and Proceedings of W.A. Parliament 1878 – 1887. Corporal Rush is referred to several times during this period in various Returns and Reports.
- 209 Batty Library, Acc. 527/243/2, Minute, 24th August 1878.

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- (h) W.A. Government Gazette 1893.
- (i) W.A. Statistical Registers 1895 – 1900.
- (j) W.A. Year Books 1872 – 1894.

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APPENDIX 1

DATE	ARMS/TYPE	QUANT.	ISSUED TO
c.1860	Enfield P.53	c.300	E.P.F.
1870	Snider-Enfield II**	250	E.P.F.
1862	Enfield P.53	200	W.A.V.F.
1864	Deane,Adams	18	W.A.P.M.V.
1870	Enfield, E.P.F.loan	c.250	W.A.V.F.
1874	Martini-Henry I	72	F.R.V.
1877	Snider III	151	M.R.V.
1877	Smith & Wesson		
	No 2	20	W.A.P.M.V.
1878	Revolvers	30	W.M.V.
1879	Snider III	50	A.R.V.
1879	Snider P.58 Naval	25	F.N.A.V.
1880	Snider-Enfield, ex E.P.F.	50	En.Guard
1880	Snider-Enfield, ex E.P.F.	c.200	W.A.V.F.
1881	Martini-Henry (II?)	28	F.R.V.
1884	Martini-Henry III	110	M.R.V.
1885	Martini-Henry II	101	W.A.V.F.
1886	Martini-Henry III	250	W.A.V.F.
1887	Martini-Henry III	60	W.A.V.F.
1895	Martini-Metford I	700	W.A.D.F.
1897	Martini-Metford II	200	W.A.M.I.
1898	Martini-Enfield I,(II?)	900	W.A.M.I.
1899	Martini-Enfield I U.C.	c.284	W.A.M.I.
1900	Martini-Enfield I, II	200	W.A.M.I.
1900	Magazine Lee-Speed	1000	W.A.I.B.
1901	Martini-Enfield II	50	
1903	Magazine Lee-Enfield I*	1350	
1903–4	Francotte Martini Cadet	1500	W.A.C.F.
1905–6	Sht.Mag. Lee-Enfield I	600	

The corps who received these arms are given where known. Where the arms were issued to several corps or throughout the Force generally they are given as W.A.V.F. or W.A.D.F. Some of the Martini-Enfields which were issued to the W.A.D.F. then passed on to the W.A.M.I. Contingents, are given as W.A.M.I. The early Federation period arms were probably issued to the W.A. Infantry Regiment and the 11th Australian Infantry Regiment, but as none have been noted these issues are omitted.

APPENDIX 2

These various marks and numbers are the key to clarifying much valuable information regarding the quantities of arms used here and their issue to W.A. troops. They are taken from specimens noted and estimates calculated from archival sources.

Known Marks and Numbers include:

W.A. ENROLLED FORCE 1850 – 1880

W.A. ENROLLED GUARD 1880 – 1887

WA/EF 1–c.300 Pattern 1853 Enfield
WA/EF 1–250 Snider-Enfield Mk II**

W.A. PINJARRAH MOUNTED VOLUNTEERS 1862 – 1882

WAPMV 1–18 Deane, Adams Revolver-Carbine

W.A. VOLUNTEER FORCE 1861 – 1893

V/WA 1–200 Pattern 1853 Enfield
V/WA 1–c.150 P Snider Mk III
ADR/1–c.70 Martini-Henry Mk III
MRV 1–c.125 Martini-Henry Mk II, III

W.A. DEFENCE FORCE 1893 – 1903

WADF(uncertain) Martini-Henry Mk III
WA/1–700 Martini-Metford MkI
WA/701–900 Martini-Metford MkII
WA/1–c.1100/D Martini-Enfield MkI, II
WA/1–c.50 Martini-Enfield Mk II
WA/1–1000 Magazine Lee-Speed

PERMANENT FORCE 1893 – 1903

PMF/97–110 Martini-Henry Carbine
(South Australian Mark)
WAA/1–c.30 Martini-Enfield Rifle MK I

W.A. CADET FORCE 1896 – 1903

1–1500/WACF Francotte Martini

APPENDIX 3

During the 1901 – 1903 period of Colonial/State/Commonwealth transition, arms continued to be marked "W A" on the butt and for the first time, on the breech also. Commonwealth marks may have been added at this time or after 1903. General Order 289 of 16th February 1903, and General Order 15 of 20th January 1904 gives the requirements for marking butts, e.g., "A/10/A.I.R." (A Company, 10th Regiment, Australian Infantry Regiment). Arms from other states have been noted with this mark, but as yet none from W.A. have been seen. W.A. arms would be marked "A/11/A.I.R."

The circular Commonwealth mark is: Commonwealth of Australia/Mily./Forces/ W.A. (within circle)/number.

This mark may be found on:

Magazine Lee-Enfield Mark I
Magazine Lee-Enfield Mark I*
Short, Magazine Lee-Enfield Mark I
W.W. Greener Cadet rifle
BSA Cadet rifle

After 1911, W.A. became the Fifth Military District. The marks are "5th M.D.," "5 M.D.," or "D broad arrow D/5". They stand for 5th Military District and Department of Defence/5th Military District. These marks may be found on the several variations of the Short, Magazine Lee-Enfield, various training rifles and their bayonets, and on bayonet practice "fencing muskets" and on swords.

Manuscript received 13 April 1994; accepted 20 September 1994.

Inability of salamanderfish, *Lepidogalaxias salamandroides*, to tolerate hypoxic water

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The salamanderfish, *Lepidogalaxias salamandroides*, is the sole member of the Osmeriform family Lepidogalaxiidae and is only found in the southwest corner of Western Australia. The preferred habitat of this small (maximum SL 67 mm) fish includes freshwater pools that evaporate during the summer (Allen and Berra 1989). Salamanderfish survive the desiccation of their habitat by burrowing into the damp substrate and remaining moist as the groundwater retreats from the surface. The fishes emerge from the bottom within minutes after autumn rains partially fill the dry pools (Berra and Allen 1989).

A recent study demonstrated that salamanderfish have the ability to exchange O₂ and CO₂ through their skin while out of water as long as they remain moist. Martin et al. (1993) showed that during aerial respiration an average of 83% of the VO₂ and 69% of the VCO₂ exchange took place across the posterior cutaneous surfaces. This high level of cutaneous respiration confirms that the swimbladder is not used as an accessory aerial respiratory structure (Berra et al. 1989).

In order to determine if salamanderfish have any special ability to tolerate low O₂ conditions in water the following experiment was conducted at the Western Australian Museum in October 1988 with newly collected salamanderfish from Station 22 (Berra and Allen 1989) and other species from a nearby stream.

Nitrogen gas was bubbled through 1 l of aquarium water at 19°C via an air stone at a pressure of less than 3 psi in order to remove dissolved oxygen. Four trials were run, in which *L. salamandroides* (N=6, \bar{x} SL = 30 mm) was compared with three other fish species (*Edelia vittata* (N=1, SL = 34 mm), *Galaxias occidentalis* (N=3, \bar{x} SL=70 mm), and *Galaxiella nigrostriata* (N=6, \bar{x} SL=28)). A polarographic oxygen probe connected to an air-calibrated ICM type 30 oxygen meter (accuracy: \pm 2%) was immersed in the water, and the dissolved oxygen levels were recorded. The reactions of the fishes were observed; when they exhibited signs of ataxia, they were removed to fresh oxygenated water.

Dissolved O₂ at the beginning of each experiment was 6–7 ppm. The fishes swam normally or sat on the bottom in the case of *Lepidogalaxias* until O₂ levels reached approximately 1.0 ppm. In most

cases this occurred within 5 minutes. At 1 ppm, all fishes began leaping and gulping air at the surface. Approximately 2–3 minutes after the O₂ tension reached 0.8 ppm all species became ataxic. They lost the ability to right themselves and lay on their sides on the bottom. At this point the fishes were removed to fresh aerated water. All recovered and were swimming normally within a few minutes. There was no noticeable difference in the reaction of *Lepidogalaxias* and the other species. The smallest fish of each species was the first to succumb; *Galaxiella* appeared to tolerate the low pO₂ slightly longer than the other 3 species.

We conclude that salamanderfish have no special ability to tolerate hypoxic water. The ability to survive in their ephemeral habitat depends upon burrowing into the substrate and remaining damp on the water table below the surface during times of drought. During this time the fish presumably enter a lowered metabolic state and respire cutaneously. The nature of this aestivation and what environmental cues trigger it remain to be determined.

ACKNOWLEDGEMENT

We thank Clay Bryce for technical assistance with the nitrogen apparatus.

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New records of fishes for the Rowley Shoals and Scott/Seringapatam Reefs, off north-western Australia

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The Rowley Shoals and Scott/Seringapatam Reefs are located off the north-western coastline of Western Australia. Staff of the Western Australian Museum have made several collecting trips to these areas (Berry 1986). Fish lists from these surveys have been published in Allen and Russell (1986) and Allen (1993) – these report a total of 688 species for the two areas.

In September/October, 1993, members of the Australian Institute of Marine Science (AIMS) visited this region to conduct visual surveys of its reef fishes as part of their investigations on the coral associated fauna of northern Australia. The senior author was invited to participate in this study because of the Western Australian Museum’s expertise in the region. Over a period of 20 days, visual surveys were made at 9–10 sites on each of the three atolls of the Rowley Shoals, 30 sites on South Scott Reef, 20 on North Scott Reef, and 11 on Seringapatam Reef (a full report of this study is in preparation). Two survey teams took part, each consisting of two SCUBA-equipped divers and a standby diver/boatperson. Each dive was usually 45 minutes long, and involved swimming along a transect that crossed from the shallowest to the deepest parts of the dive (the maximum depth worked was 20 m). Sites both inside and outside the lagoons and on the outer slopes were surveyed. In addition, several deeper water collections were made with handlines, droplines, and rod and reel.

A total of 445 species were recorded, of which 99 are new records for the Scott/Seringapatam reefs, 39 are new for the Rowley Shoals, and 23 are new records common to both areas. Of this total of 161 new records, 81 have not been recorded from

either location before, and three species are new records for Australia. The purpose of this paper is to report these new additions.

The list presented below follows the format utilised by Allen (1993) in his summary of the fish fauna of the two areas. Numerous species with questionable identities were also recorded during the study; however, only those positively identified have been included. As anticipated by Allen (1993), these additional surveys suggest a more uniform distribution of species among these reefs than the earlier study.

ACKNOWLEDGEMENTS

We would like to thank Suzanne Williams and the crew of the RV Lady Basten for their assistance. We are also grateful for comments made by G.R. Allen on an early draft of the fish list.

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List of New Fish Records

- Key to symbols:
- c = collected and retained (at WAM)
 - r = collected but not retained
 - x = visual record
 - * = new record for Australia

	Scott/ Seringapatam	Rowley Shoals
CARCHARHINIDAE		
<i>Carcharhinus albimarginatus</i> (Rüppell, 1837)	r	x
MOBULIDAE		
<i>Manta birostris</i> (Walbaum, 1792)	x	

	Scott/ Seringapatam	Rowley Shoals
MURAENIDAE		
<i>Gymnothorax javanicus</i> (Bleeker, 1865)		x
HOLOCENTRIDAE		
<i>Myripristes chryseres</i> Jordan and Evermann, 1905	c	
<i>M. murdjan</i> (Forsskål, 1775)	x	
FISTULARIIDAE		
<i>Fistularia commersoni</i> Rüppell, 1835		x
SYNGNATHIDAE		
<i>Corythoichthys intestinalis</i> (Ramsay, 1881)	x	
SCORPAENIDAE		
<i>Pterois volitans</i> (Linnaeus, 1758)	x	
SERRANIDAE		
<i>Belonoperca chabanaudi</i> Fowler and Bean, 1930		x
<i>Cephalopholis sexmaculata</i> (Rüppell, 1830)	x	x
<i>Epinephelus fuscoguttatus</i> (Forsskål, 1775)	x	x
<i>E. hexagonatus</i> (Bloch and Schneider, 1801)	x	
<i>E. lanceolatus</i> (Bloch, 1790)	x	
* <i>E. miliaris</i> (Valenciennes, 1830)	c	
<i>E. spilotoceps</i> Schultz, 1953		x
<i>Pseudanthias dispar</i> (Herre, 1955)	x	
<i>P. huchtii</i> (Bleeker, 1857)	x	
<i>P. squamipinnis</i> (Peters, 1855)	x	
<i>Variola albimarginatus</i> Baissac, 1953	r	
<i>V. louti</i> (Forsskål, 1775)	x	x
PSEUDOCROMIDAE		
<i>Congrogadus subducens</i> (Richardson, 1843)	x	
APOGONIDAE		
<i>Apogon fragilis</i> Smith, 1961	x	
<i>A. novemfasciatus</i> Cuvier, 1828	x	
* <i>A. seali</i> Fowler, 1918	x	
<i>Rhabdamia gracilis</i> (Bleeker, 1856)	x	
MALACANTHIDAE		
<i>Malacanthus brevirostris</i> Guichenot, 1848		x
<i>M. latovittatus</i> (Lacepède, 1798)	x	
ECHENEIDIDAE		
<i>Echeneis naucrates</i> Linnaeus, 1758		x
<i>Remora brachyptera</i> (Lowe, 1839)		c
<i>R. osteochir</i> (Cuvier, 1829)	c	
CARANGIDAE		
<i>Carangoides fulvoguttatus</i> (Forsskål, 1775)	x	
<i>C. orthogrammus</i> (Jordan and Gilbert, 1882)	x	x
<i>C. plagiotaenia</i> Bleeker, 1857	x	x
<i>Caranx lugubris</i> Poey, 1860	r	
<i>C. sexfasciatus</i> Quoy and Gaimard, 1825		x
<i>Elagatis bipinnulatus</i> (Quoy and Gaimard, 1825)	r	
<i>Scomberoides lysan</i> (Forsskål, 1775)		x
<i>Trachinotus blochii</i> (Lacepède, 1801)		x
CAESIONIDAE		
<i>Caesio cuning</i> (Bloch, 1791)	x	
<i>C. lunaris</i> Cuvier, 1830	x	
<i>Pterocaesio trilineata</i> Carpenter, 1987	x	
LUTJANIDAE		
<i>Aphareus rutilans</i> Cuvier, 1830	x	
<i>Aprion virescens</i> Valenciennes, 1830	x	

	Scott/ Seringapatam	Rowley Shoals
<i>Lutjanus fulvus</i> (Bloch and Schneider, 1801)	x	
<i>Macolor macularis</i> Fowler, 1931	x	
<i>M. niger</i> (Forsskål, 1775)	r	
<i>Symphorus nematophorus</i> (Bleeker, 1860)	x	
HAEMULIDAE		
<i>Plectorhinchus goldmanni</i> Bleeker, 1853	x	
<i>P. diagrammus</i> Linnaeus, 1758	x	
LETHRINIDAE		
<i>Gymnocranius microdon</i> (Bleeker, 1851)	x	
<i>Lethrinus erythracanthus</i> Valenciennes, 1830	r	x
<i>L. erythropterus</i> Valenciennes, 1830	r	x
<i>L. microdon</i> Valenciennes, 1830	r	
<i>L. obsoletus</i> (Forsskål, 1775)		x
<i>L. rubrioperculatus</i> Sato, 1978		r
<i>L. xanthochilus</i> Klunzinger, 1870	r	r
MULLIDAE		
<i>Parupeneus barberinoides</i> (Bleeker, 1852)	x	
<i>P. cyclostomus</i> (Lacepède, 1802)	x	
<i>P. pleurostigma</i> (Bennett, 1830)	x	
KYPHOSIDAE		
<i>Kyphosus bigibbus</i> (Lacepède, 1801)	x	
<i>K. cinerascens</i> (Forsskål, 1775)	x	x
<i>K. vaigiensis</i> (Quoy and Gaimard, 1824)	x	x
EPHIPPIDAE		
<i>P. pinnatus</i> (Linnaeus, 1758)	x	x
<i>Platax teira</i> (Forsskål, 1775)	x	
CHAETODONTIDAE		
<i>Chaetodon lineolatus</i> Cuvier, 1831	x	
<i>C. meyeri</i> Bloch and Schneider, 1801		x
<i>C. ocellicaudus</i> Cuvier, 1831	x	
<i>C. octofasciatus</i> Bloch, 1787	x	
<i>C. unimaculatus</i> Bloch, 1787	x	
<i>C. vagabundus</i> Linnaeus, 1758		x
<i>Forcipiger longirostris</i> (Broussonet, 1782)	x	
<i>Heniochus singularius</i> Smith and Radcliffe, 1911	x	
POMACANTHIDAE		
<i>Centropyge eibli</i> Klausewitz, 1963	x	
<i>Pomacanthus imperator</i> (Bloch, 1787)		x
POMACENTRIDAE		
<i>Amblyglyphidodon curacao</i> (Bloch, 1787)	x	
<i>Amphiprion perideraion</i> Bleeker, 1855	x	
<i>A. sandaracinos</i> Allen, 1972	x	
<i>Chromis amboinensis</i> (Bleeker, 1873)	x	
<i>C. lepidolepis</i> Bleeker, 1877	x	
<i>C. lineata</i> Fowler and Bean, 1928	x	
<i>C. retrofasciata</i> Weber, 1913	x	
<i>C. viridis</i> (Cuvier, 1830)	x	
<i>Chrysiptera talboti</i> (Allen, 1975)	x	
<i>Pomacentrus coelestis</i> Jordan and Starks, 1901	x	
<i>P. nigromanus</i> Weber, 1913		x
<i>P. nigromarginatus</i> Allen, 1973	x	
<i>Premnas biaculeatus</i> (Bloch, 1790)	x	
<i>Stegastes fasciolatus</i> (Ogilby, 1889)	x	
CIRRHITIDAE		
<i>Cirrhitus pinnulatus</i> (Schneider, 1801)	x	

	Scott/ Seringapatam	Rowley Shoals
SPHYRAENIDAE		
<i>Sphyraena flavicauda</i> Rüppell, 1838		x
LABRIDAE		
<i>Anampses geographicus</i> Valenciennes, 1840	x	x
<i>A. meleagrides</i> Valenciennes, 1840	x	
<i>A. twistii</i> Bleeker, 1856	x	x
<i>Bodianus diana</i> (Lacepède, 1801)		x
<i>B. mesothorax</i> (Bloch and Schneider, 1801)	x	
<i>Cheilinus bimaculatus</i> Valenciennes, 1840	x	
<i>C. oxycephalus</i> Bleeker, 1853	x	x
<i>C. unifasciatus</i> Streets, 1877	x	
<i>Cheilio inermis</i> (Forsskål, 1775)	x	x
<i>Cirrhitilabrus exquisitus</i> Smith, 1957	x	
<i>Cymolutes praetextatus</i> (Quoy and Gaimard, 1834)	x	
<i>Halichoeres hartzfeldi</i> Bleeker, 1852		x
<i>H. scapularis</i> (Bennett, 1831)	x	
<i>Hemigymnus fasciatus</i> (Bloch, 1792)		x
<i>Hologymnosus doliatus</i> (Lacepède, 1801)	x	
<i>Labroides bicolor</i> Fowler and Bean, 1928	x	
<i>Labropsis manabei</i> Schmidt, 1930		x
<i>Macropharyngodon meleagris</i> (Valenciennes, 1839)		x
<i>M. negrosensis</i> Herre, 1932	x	
<i>Novaculichthys taeniourus</i> (Lacepède, 1801)		x
<i>Pseudocheilinus octotaenia</i> Jenkins, 1900	x	
<i>Thalassoma janssenii</i> (Bleeker, 1856)	x	
<i>T. lunare</i> (Linnaeus, 1758)		x
<i>T. purpureum</i> (Forsskål, 1775)	x	
SCARIDAE		
<i>Bolbometopon muricatum</i> (Valenciennes, 1840)	x	
<i>Leptoscarus vaigiensis</i> (Quoy and Gaimard, 1824)	x	
* <i>Scarus atropectoralis</i> Schultz, 1958	x	x
<i>S. bleekeri</i> (de Beaufort, 1940)		x
<i>S. dimidiatus</i> Bleeker, 1859		x
<i>S. forsteni</i> (Bleeker, 1861)		x
<i>S. ghobban</i> Forsskål, 1775	x	
<i>S. globiceps</i> Valenciennes, 1840	x	
<i>S. niger</i> Forsskål, 1775		x
<i>S. oviceps</i> Valenciennes, 1840	x	
<i>S. prasiognathus</i> Valenciennes, 1840	x	
<i>S. schlegelii</i> (Bleeker, 1861)	x	x
<i>S. spinus</i> (Kner, 1868)	x	
PINGUIPEDIDAE		
<i>Parapercis clathrata</i> Ogilby, 1911	x	
GOBIIDAE		
<i>Amblyeleotris steinitzi</i> (Klausewitz, 1974)	x	
<i>Amblygobius phalaena</i> (Valenciennes, 1837)	x	
<i>Istigobius rigilius</i> (Herre, 1953)	x	
<i>Signigobius biocellatus</i> Hoesé and Allen, 1977	x	
<i>Valenciennaea longipinnis</i> (Lay and Bennett, 1839)	x	
<i>V. sexguttata</i> (Valenciennes, 1837)	x	
<i>V. strigata</i> (Broussonet, 1782)		x
MICRODESMIDAE		
<i>Ptereleotris zebra</i> Fowler, 1938	x	
ACANTHURIDAE		
<i>Acanthurus nigrocauda</i> Duncker and Mohr, 1929	x	
<i>Ctenochaetus strigosus</i> (Bennett, 1828)		x
<i>Naso brachycentron</i> (Valenciennes, 1835)	x	
<i>N. tuberosus</i> Lacepède, 1802	x	

	Scott/ Seringapatam	Rowley Shoals
ZANCLIDAE		
<i>Zanclus cornutus</i> (Linnaeus, 1758)	x	
SIGANIDAE		
<i>Siganus argenteus</i> (Quoy and Gaimard, 1825)	x	x
<i>S. corallinus</i> (Valenciennes, 1835)	x	x
<i>S. punctatissimus</i> Fowler and Bean, 1929		x
<i>Siganus punctatus</i> (Forster, 1801)	x	x
SCOMBRIDAE		
<i>Euthynnus affinis</i> (Cantor, 1849)	x	
<i>Grammatorcynus bilineatus</i> (Rüppell, 1836)		x
ISTIOPHORIDAE		
<i>Istiophorus platypterus</i> (Shaw and Nodder, 1792)	r	
BOTHIDAE		
<i>Bothus pantherinus</i> (Rüppell, 1828)		x
BALISTIDAE		
<i>Odonus niger</i> Rüppell, 1836	x	
<i>Pseudobalistes flavimarginatus</i> Rüppell, 1829		x
MONACANTHIDAE		
<i>Acreichthys radiatus</i> (Popta, 1901)		x
<i>Aluterus scriptus</i> (Osbeck, 1765)	x	x
<i>Amanes scopas</i> Cuvier, 1829		x
<i>Cantherhines dumerilii</i> (Hollard, 1854)		x
<i>C. pardalis</i> (Rüppell, 1837)		x
<i>Oxymonacanthus longirostris</i> (Bloch and Schneider, 1801)		x
<i>Paraluteres prionurus</i> (Bleeker, 1851)	x	x
TETRAODONTIDAE		
<i>Arothron stellatus</i> (Bloch and Schneider, 1801)	x	
<i>Canthigaster bennetti</i> (Bleeker, 1854)	x	
DIODONTIDAE		
<i>Diodon liturosus</i> Shaw, 1804	x	

Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance an IBM compatible disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. WordPerfect, Wordstar, etc).

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The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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Records of the Western Australian Museum



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Volume 17 Part 2 1995

Records of the Western Australian Museum

The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

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Printed and published by the Western Australian Museum
© Western Australian Museum, June 1995
ISSN 0312 3162

Cover: The weevil *Catasarcus militaris* Peterson, 1995.
Illustration by Magnus Peterson.



Systematic review of *Nyctimene cephalotes* and *N. albiventer* (Chiroptera: Pteropodidae) in the Maluku and Sulawesi regions, Indonesia

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Abstract – A univariate and multivariate statistical study of the morphology of island populations of *Nyctimene* in the Maluku region, Indonesia, distinguishes *Nyctimene keasti* Kitchener, 1993, from the Tanimbar and Kai Islands, as a species. The form from the Tanimbar islands is described as a new subspecies of *N. keasti*; it is not associated with *N. cephalotes* as previously considered in litt. *Nyctimene cephalotes* is restricted to Sulawesi and the Maluku region. The Sulawesi population of *N. cephalotes* is described as a distinct new subspecies. The Aru population of *N. albiventer* is somewhat differentiated from the Papua New Guinea population of *N. a. papuanus*; its subspecific status is not determined.

Close island populations of *N. c. cephalotes*, *N. k. keasti* and *N. k. subsp. nov.* show considerable morphological differentiation.

INTRODUCTION

Kitchener *et al.* (1993) examined morphological variation among populations of *Nyctimene albiventer* (Gray, 1863) in the Maluku region. They showed that the population on Aru was morphologically similar to the Papua New Guinea *N. a. papuanus* K. Andersen, 1910; while those on the Kai and Banda Neira Islands (*N. a. keasti* Kitchener, 1993) were distinct from both the Aru form and the nominate subspecies on Halmahera and Ternate Islands.

The discovery of *N. a. keasti* confuses somewhat the previous diagnostic distinction between *N. albiventer* and the closely allied *N. cephalotes* (Pallas, 1767). This distinction had been based on the larger size of *N. cephalotes* and the fact that the females had a dorsum that was much paler than the males, whereas in *N. albiventer* there was no such colour distinction between the sexes (Anderson 1912). A number of *Nyctimene a. keasti* specimens had forearm lengths overlapping those of both *N. a. albiventer* and *N. cephalotes*. Further, female *N. a. keasti* were much paler dorsally than the males.

In the study region, *N. cephalotes* is reported from the following islands: Ambon (fixed as the type locality by Andersen 1912); Seram; Buru, Larat Island (Tanimbar group); Timor and Sulawesi (Andersen 1912; Hill in Corbet and Hill 1992). The records from Larat Island and Timor Island appear to devolve on single specimens collected late last century (Andersen 1912, Goodwin 1979).

Between 1987 and 1993 expeditions by staff from the Western Australian Museum and Museum Zoologicum Bogoriense carried out a survey of the

terrestrial vertebrate fauna of South Sulawesi, Maluku and Nusa Tenggara, Indonesia. On these expeditions, series of *Nyctimene* that would be attributed to *N. cephalotes* by earlier authors, were collected from the following islands: Seram; Ambon; Buru; Yamdena and Selaru, Tanimbar group; and South Sulawesi. This paper reports on an examination of these extensive modern collections which allow both a re-appraisal of morphological variation among island populations of *N. cephalotes* and *N. albiventer* and a reassessment of their taxonomy in the study region.

MATERIALS AND METHODS

A total of 142 adult specimens (listed in specimens examined section) was examined. These were from Banda Neira Neira I. (2); Dullah I., Kai Kecil (7); Kai Besar I. (5); Wokam I., Aru islands (27); the Halmahera group (6); Papua New Guinea (13); Ambon (10); Seram (16); Buru (2); Sulawesi (9); Selaru (13) and Yamdena (32). The localities of these specimens are shown in Figure 1. Apart from the Halmahera group specimens (Australian Museum, Sydney), all specimens are currently lodged in the Western Australian Museum.

Seventeen measurements of skull, dentary and dental characters and six of external body characters (all in mm) were recorded from adult specimens.

The measurements recorded were (all measurement involving teeth were to alveoli): GSL,

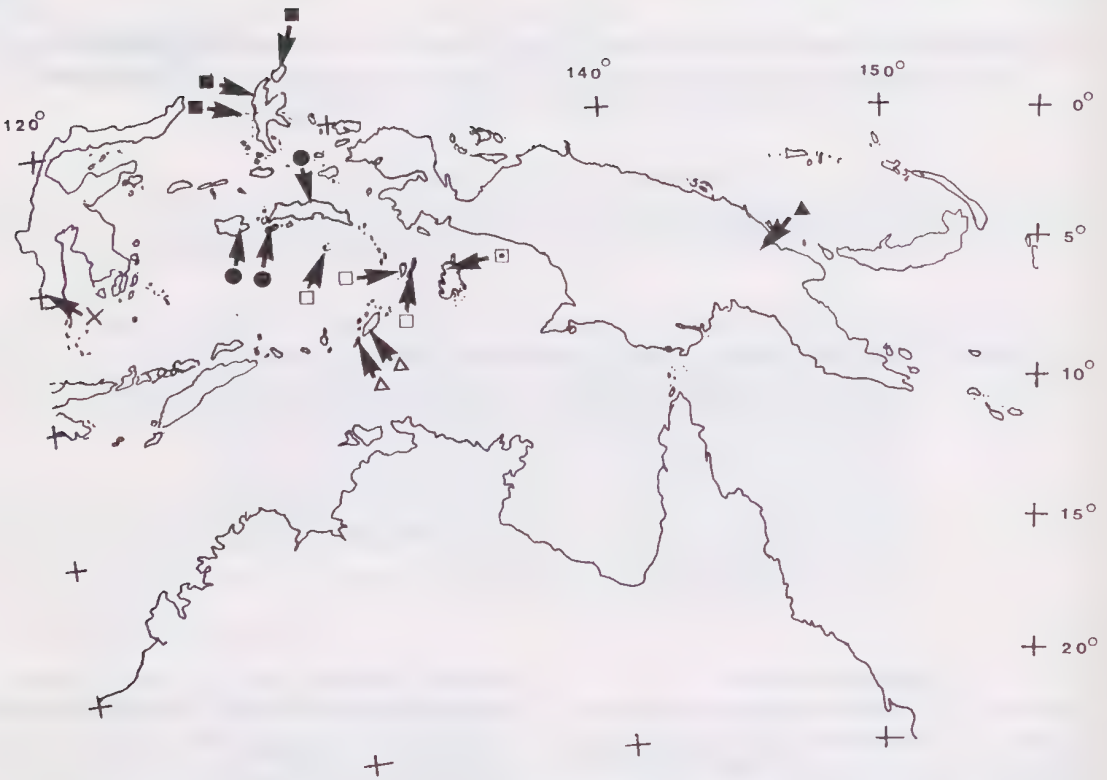


Figure 1 Locality of *Nyctimene* in this study; *N. albiventer albiventer*, ■; *N. a. subsp. indet.*, □; *N. a. papuanus*, ▲; *N. keasti keasti*, ◻; *N. k. tozeri subsp. nov.*, △; *N. cephalotes cephalotes*, ●; *N. c. aplini subsp. nov.*, X.

greatest skull length; CBL, condylobasal length; PIF, minimum length from posterior margin of incisive foramen to palate posterior margin; RL, rostrum length, from anteriormost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M¹M¹ and C¹C¹, width across M¹M¹ and C¹C¹ respectively, from the labial side; C¹M¹ and C₁M₂, upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFB, mesopterygoid fossa breadth, at the widest point of the palatal flange; P⁴P⁴, palatal width between the lingual aspect of P⁴P⁴; ML, mandible length, from condyle to anteriormost point of dentary; CH, dentary coronoid height; TV, tail to anus length; EAR, basal notch to apex length; FA, forearm length; and MC3–5, metacarpal 3, 4 and 5 length.

The skull, dentary and dental characters were measured to an accuracy of 0.01 mm, while the external body characters were measured to 0.1 mm. Terminology used in the description of skull, dentary, dental and external body characters follows Hill and Smith (1984). Pelage descriptions follow the colour terminology of Smith (1975).

Adults were diagnosed as those specimens with the following sutures fused: basioccipital – basisphenoid, basisphenoid – presphenoid and palatine – maxillary (these sutures are illustrated in Heaney and Peterson 1984: Figure 4).

The effect of sex and island on all characters was examined by multiple regressions for the islands: Yamdena, Selaru, Kai Kecil, Kai Besar, Aru, Ambon, Seram, Sulawesi and Papua New Guinea. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Stepwise canonical variate (discriminant function) analyses (DFA) were run for skull, dentary and dental characters and external characters using all 23 characters for males and females combined, after first testing for sexual dimorphism. A reduced set of five of these characters was used in all presented DFA because in all instances they provided similar DF plots to the full set of 23 characters. This reduced set of characters was selected in all these analyses because the sample size of the smallest *a priori* group selected was always less than the total number of characters. This reduced set of characters was selected because they provided values that minimise Wilk's Lambda.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island are presented in Table 1, this paper, and Kitchener *et al.* (1993: Table 1) for all characters examined.

Multiple regressions

Multiple regressions were run for skull, dentary, dental and external characters on sex and nine island populations. The islands of Buru, Banda Neira, Halmahera, Ternate and Morotai were excluded because of their small sample size and/or absence of either males or females (Table 2).

Sex

Metacarpal 3–5 lengths and postorbital breadth were significantly influenced by sex ($F_{1,96} = 6.11$, $P = 0.015$; $F_{1,96} = 4.67$, $P = 0.033$; $F_{1,96} = 4.653$, $P = 0.033$; and $F_{1,96} = 4.639$, $P = 0.034$, respectively).

Island

Only postorbital breadth was not highly (<0.01) significantly related to island. Clearly there was considerable difference in morphology between these island populations.

Interactions

There were no significant interactions.

Multivariate analyses

Because the multiple regression analysis involved testing a large number of interactions, some of these tests will be significant at $0.05 > P > 0.01$ by chance alone. For this reason, none of the characters measured were considered to be markedly influenced by sex. As a result both males and females are combined for all 23 characters examined in the following DFA.

All populations

The DFA was first run using all 23 skull, dental, dentary and external body characters and the islands Aru, Kai Besar, Kai Kecil, the Halmahera group (Halmahera, Ternate and Morotai) Papua New Guinea, Selaru and Yamdena (Tanimbar Islands), Seram, Ambon and Sulawesi. Banda Neira and Buru were ungrouped because there were only two individuals from each of these islands. The above analysis was then repeated using only five characters (forearm length, FA; ear length EAR; C_1M_2 length, C_1M_2 ; width across M'M' from labial side, M'M'; and rostral length, RL). This analysis extracted four significant functions which together explained 99.6% of the variation, with 68.0% of individuals classified to their correct island group.

From Figure 2, three broad groups were defined:

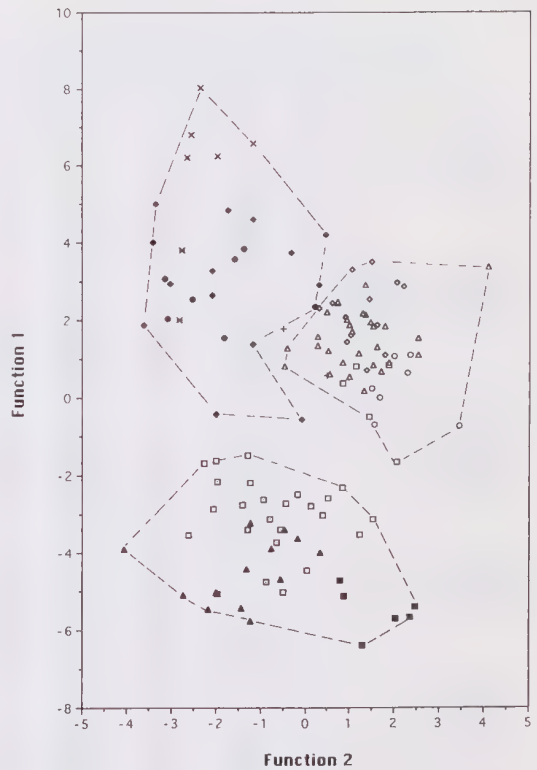


Figure 2 Canonical variate analysis on the following island populations: Aru, \square ; Kai Besar, \square ; Kai Kecil, \circ ; the Halmahera group (Halmahera, Ternate and Morotai), \blacksquare ; Papua New Guinea, \blacktriangle ; Selaru \diamond ; and Yamdena, \triangle (Tanimbar group); Seram, \blacklozenge ; Ambon, \bullet ; and Sulawesi, \times ; Banda Beira $+$, and Buru $*$, were ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five characters (skull, dentary, and external body), with males and females combined.

the Ambon group (Ambon-Seram-Buru-Sulawesi); the Kai group (Kai and Tanimbar islands); and the Halmahera group (Halmahera, Aru and Papua New Guinea). When a DFA was again run using the reduced set of five characters and these three island groups, the analysis extracted two significant functions (Figure 3). Function 1, which explained 78.9% of the variance, separated the Ambon and Kai groups from the Halmahera group. The character loading heavily on the standardised canonical variate coefficients (>0.6) on this function was C_1M_2 length (Table 3). Function 2, which separated the Ambon group from the Kai group, explained 21.1% of the variation. The characters loading heaviest (>0.6) on Function 2 were forearm and ear length (Table 3). A total of 99.2% of individuals was correctly classified to their appropriate island group. One specimen of the Ambon group classified to the Kai

Table 1 Measurements, in mm, for skull, dentary, dental and external body characters (see Material and Methods section for explanation of character codes) of adult *Nyctimene cephalotes aplini*, *N. c. cephalotes*, *N. keasti keasti* and *N. k. tozeri*. N, sample size; \bar{X} , mean; SD, standard deviation; MIN, minimum; MAX, maximum.

		GSL	CBL	PIF	RL	RH	BB	ZW	M'M ¹	C'C ¹
<i>Nyctimene cephalotes aplini</i> (Sulawesi)	N	9	9	9	9	9	9	9	9	9
	\bar{X}	31.74	30.22	12.77	6.39	7.25	13.40	21.37	9.56	5.80
	SD	0.47	0.33	1.48	0.39	0.27	0.27	0.48	0.19	0.27
	MIN	31.05	29.71	11.76	5.72	6.64	12.95	20.74	9.31	5.43
	MAX	32.42	30.67	13.54	7.00	7.59	13.81	22.24	9.92	6.17
<i>N. cephalotes cephalotes</i> (Seram, Ambon, Buru)	N	25	25	26	26	26	26	26	26	26
	\bar{X}	30.13	28.66	12.23	5.94	7.05	12.76	19.80	8.88	5.57
	SD	0.68	0.64	0.48	0.27	0.34	0.37	0.72	0.32	0.24
	MIN	28.32	26.98	11.45	5.27	6.16	11.59	17.81	7.81	5.04
	MAX	31.05	29.69	13.70	6.39	7.79	13.39	20.90	9.42	6.02
<i>N. cephalotes</i> (Sulawesi, Seram, Ambon, Buru)	N	34	34	35	35	35	35	35	35	35
	\bar{X}	30.56	29.07	12.37	6.06	7.10	12.93	20.21	9.06	5.63
	SD	0.95	0.90	0.53	0.36	0.33	0.44	0.96	0.42	0.26
	MIN	28.32	26.98	11.45	5.27	6.16	11.59	17.81	7.81	5.04
	MAX	32.42	30.67	13.70	7.00	7.79	13.81	22.24	9.92	6.17
<i>N. keasti keasti</i> (Kai Besar, Kai Kecil)	N	12	12	12	12	12	12	12	12	12
	\bar{X}	28.77	27.28	12.06	5.52	6.36	12.34	19.06	8.16	5.46
	SD	0.50	0.52	0.26	0.34	0.37	0.31	0.33	0.24	0.24
	MIN	28.04	26.02	11.58	4.96	5.75	11.64	18.63	7.66	5.18
	MAX	29.38	27.88	12.47	6.00	6.96	12.68	19.71	8.45	5.80
<i>N. keasti tozeri</i> (Selaru, Yamdena)	N	44	44	44	44	44	44	44	44	44
	\bar{X}	29.50	27.74	11.85	5.73	6.72	12.72	19.34	8.70	5.57
	SD	0.56	0.48	0.43	0.27	0.28	0.28	0.45	0.23	0.18
	MIN	28.45	26.64	10.92	5.07	6.22	12.20	18.11	8.09	5.24
	MAX	30.78	28.74	12.81	6.30	7.30	13.94	20.40	9.09	5.96
<i>N. keasti</i> (Kai Is, Tanimbar Is)	N	56	56	56	56	56	56	56	56	56
	\bar{X}	29.35	27.65	11.91	5.68	6.64	12.64	19.28	8.58	5.55
	SD	0.62	0.52	0.41	0.30	0.33	0.33	0.44	0.32	0.20
	MIN	28.04	26.02	10.92	4.96	5.75	11.64	18.11	7.66	5.18
	MAX	30.78	28.74	12.81	6.30	7.30	13.94	20.40	9.09	5.96

group. Of the two “ungrouped” Banda Neira specimens, both classified to the Kai group.

These three island groups represent three described taxa as will be discussed below. These taxa are *Nyctimene cephalotes* (Ambon, Seram, Buru, Sulawesi); *N. keasti* (Kai and Tanimbar groups, with Banda Neira specimens referred to this group); and *N. albiventer* (Halmahera, Aru and Papua New Guinea).

Nyctimene cephalotes populations

A DFA was run for all 23 characters for the islands Ambon, Seram and Sulawesi, with Buru unallocated. A reduced set of five characters was selected from this above analysis. These were: condylobasal length, CBL; zygomatic width, ZW; mesopterygoid fossa breadth, MFB; mandible length, ML; and upper canine to first molar cusp length, C'M¹. The selection of only skull and mandible characters in this subset of five characters enabled the inclusion of an additional sample of Sulawesi individuals (which were missing some

external measurements) to be included in this DFA. This latter DFA extracted two significant functions which explained 100% of the variation (Figure 4). A total of 73.5% of individuals was correctly classified to their correct island population, with misclassification occurring between the Ambon and Seram populations. One of the Buru specimens was allocated by DFA to the Seram population and the other to the Ambon population.

The DFA was run again using 23 characters for the two *a priori* groups: Sulawesi and the group Ambon, Seram and Buru. A subset of five characters (condylobasal length; C'M¹ length; M'M¹ breadth; rostrum height; incisive foramen to posterior palatal length) was selected from the above analysis. This latter analysis extracted a very significant function and all individuals were correctly classified to their appropriate group (Figure 5). The characters loading most heavily on this function were CBL (1.9), C'M¹ (−1.4) and M'M¹ (0.6) (Table 4).

The type locality of the nominate subspecies of

Table 1 (continued)

C'M'	IOB	POB	MFB	P ^a P ^a	ML	CH	C ₁ M ₂	FA	MC3	MC4	MC5	TV	EAR
9	9	9	9	9	9	9	9	5	5	5	5	5	5
10.62	6.44	6.18	5.18	6.02	23.79	13.92	11.96	68.6	49.1	44.8	48.6	25.1	16.2
0.28	0.40	0.60	0.13	0.23	0.41	0.31	0.25	0.6	1.9	2.2	2.7	1.0	0.3
10.34	6.03	5.51	4.96	5.47	23.20	13.41	11.66	68.1	47.4	42.3	45.2	23.7	15.8
11.11	7.17	7.39	5.37	6.26	24.37	14.47	12.41	69.5	51.8	47.7	52.0	26.2	16.5
26	26	26	25	26	26	26	26	24	24	24	24	24	24
10.16	5.65	5.77	5.16	5.58	22.55	12.99	11.46	63.4	45.1	41.8	44.6	22.4	14.2
0.43	0.35	0.44	0.20	0.23	0.67	0.72	0.44	2.1	1.6	1.5	1.7	1.3	0.6
9.02	4.94	5.17	4.79	4.89	21.02	11.47	10.21	59.1	41.4	38.6	40.2	20.6	12.9
10.82	6.13	6.94	5.61	5.94	23.69	14.23	12.09	67.6	48.0	44.1	47.2	24.8	15.2
35	35	35	34	35	35	35	35	29	29	29	29	29	29
10.28	5.85	5.88	5.16	5.69	22.87	13.23	11.59	64.3	45.8	42.3	45.3	22.9	14.5
0.44	0.50	0.51	0.19	0.30	0.82	0.76	0.46	2.7	2.2	2.0	2.4	1.6	1.0
9.02	4.94	5.17	4.79	4.89	21.02	11.47	10.21	59.1	41.4	38.6	40.2	20.6	12.9
11.11	7.17	7.39	5.61	6.26	24.37	14.47	12.41	69.5	51.8	47.7	52.0	26.2	16.5
12	12	12	12	12	12	12	12	12	12	12	12	12	12
9.57	5.69	6.02	4.76	5.19	21.49	12.86	10.84	58.2	42.2	38.5	40.6	20.7	15.0
0.24	0.24	0.35	0.17	0.10	0.51	0.31	0.26	1.3	1.1	0.7	1.0	1.5	0.5
8.98	5.29	5.21	4.50	5.03	20.58	12.33	10.27	55.1	40.7	37.5	38.7	18.6	14.2
9.80	6.12	6.44	5.05	5.38	22.11	13.32	11.18	59.7	44.5	39.6	42.7	24.1	15.6
44	44	44	44	44	44	44	44	44	44	44	44	44	44
10.01	5.81	5.66	5.00	5.60	22.00	13.38	11.28	60.1	43.5	39.6	42.1	21.3	15.4
0.33	0.28	0.41	0.17	0.19	0.49	0.47	0.29	1.2	1.0	1.1	1.0	1.6	0.6
8.39	5.30	5.03	4.56	5.24	21.04	12.34	10.76	58.0	41.6	37.5	40.0	18.0	14.3
10.50	6.49	6.65	5.39	5.97	23.10	14.46	12.10	63.0	45.7	43.1	44.2	25.4	16.9
56	56	56	56	56	56	54	56	56	56	56	56	56	56
9.91	5.78	5.74	4.95	5.51	21.89	13.26	11.18	59.7	43.2	39.4	41.8	21.2	15.3
0.36	0.27	0.42	0.20	0.24	0.53	0.49	0.34	1.4	1.2	1.1	1.2	1.6	0.6
8.39	5.29	5.03	4.50	5.03	20.58	12.33	10.27	55.1	40.7	37.5	38.7	18.0	14.2
10.50	6.49	6.65	5.39	5.97	23.10	14.46	12.10	63.0	45.7	43.1	44.2	25.4	16.9

N. cephalotes was fixed as Ambon by Andersen (1912). The above documentation of the morphological separation of the Sulawesi population from *N. c. cephalotes* warrants its description as a new subspecies of *N. cephalotes*.

Nyctimene keasti populations

DFA was run for all 23 characters for the islands Kai Besar, Kai Kecil, Selaru and Yamdena, with Banda Neira unallocated. A reduced set of five characters was selected from this above analysis. These were palatal width between the lingual aspect of P^aP^a; ear length; forearm length; braincase breadth; minimum length from posterior margin of incisive foramen to palate posterior margin. This latter DFA produced two significant functions, which combined explained 98.4% of the variation (Figure 6). A total of 81.5% of individuals were correctly classified to their appropriate island, with misclassification occurring between the two Tanimbar islands. One of the unallocated Banda Neira specimens classified with the Selaru

population and the other with the Yamdena population.

The DFA run with 23 characters and only two *a priori* groups: Tanimbar group (Selaru and Yamdena) and Kai group (Kai Kecil and Kai Besar) produced a similar discriminant histogram to that produced from a subset of the five characters that were selected from the above analysis (palate breadth at P^aP^a; incisive foramen to posterior palate length, PIF; braincase breadth, BB; postorbital breadth, POB; and forearm length, FA). The function extracted from this latter analysis was highly significant and resulted in all individuals being correctly allocated to their appropriate group (Figure 7). The characters loading heavily (>0.6) on this function were P^aP^a, FA and BB (Table 5).

The type locality of the nominate subspecies of *N. keasti* is Pulau Dullah, Kai Kecil. The above analysis documents clearly the morphological separation of the Tanimbar form from *N. k. keasti*. It indicates that the Tanimbar form warrants description as a new taxon. It also shows that some

Table 2 Multiple regressions on sex and island populations of *Nyctimene albiventer*, *N. cephalotes* and *N. keasti* for skull, dentary, dental and external body characters. F values are presented for the main effects and their interactions. For explanation of character codes see Material and Methods section. Significance levels are *, 0.05>p>0.01; ** 0.01>p>0.001; ***, p<0.001.

CHARACTER	MAIN EFFECT		INTERACTION SEX, ISLAND
	SEX	ISLAND	
GSL	0.354	54.340***	0.774
CBL	0.050	45.776***	0.968
PIF	0.646	27.866***	0.831
RL	0.530	41.475***	0.911
RH	0.015	10.427***	0.795
BB	0.335	17.716***	0.817
ZW	0.618	26.450***	0.877
M¹M¹	0.367	17.584***	0.774
C¹C¹	1.770	5.361***	1.378
C¹M¹	0.083	32.995***	0.430
IOB	0.110	15.210***	1.012
POB	4.631*	0.959	0.875
MFB	0.000	16.366***	0.376
P¹P¹	2.096	6.823***	0.367
ML	0.063	41.255***	0.425
CH	0.010	28.720***	1.173
C₁M₂	0.084	45.256***	0.695
FA	1.887	62.079***	0.725
MC3	6.110*	42.895***	0.914
MC4	4.667*	46.285***	1.117
MC5	4.653*	41.120***	1.070
TV	2.469	3.331**	0.818
EAR	0.422	30.529***	0.571
d.f.	1,96	8,96	8,96

morphological differentiation has occurred between the two Kai Island populations.

***Nyctimene albiventer* populations**

Kitchener *et al.* (1993) examined the morphological differences between the Halmahera group (*N. a. albiventer*), Aru and Papua New Guinea populations (attributed to *N. a. papuanus*)

Table 3 Canonical variate function coefficients from DFA between the *Nyctimene* species (*N. albiventer*, *N. cephalotes* and *N. keasti*). Standardised values, followed by (in brackets) unstandardised values, for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1	FUNCTION 2
C₁M₂	0.6941 (1.7737)	0.5583 (1.4266)
FA	0.4366 (0.2167)	-0.8945 (-0.4438)
EAR	-0.0297 (-0.0373)	0.9784 (1.2309)
RL	0.4542 (1.5569)	-0.0234 (-0.0802)
M¹M¹	-0.4455 (-1.1545)	-0.4087 (-1.0591)
Constant	-30.0241	2.4944
Explained variation (%)	78.9	21.1

and Kai group (*N. a. keasti*) populations. The removal of the form *keasti* from association with *N. albiventer* in this study may affect the perceived morphological association between these remaining populations of *N. albiventer* using DFA.

DFA was run on all 23 characters for the islands: Halmahera, Aru and PNG. A reduced set of five characters was selected from the above analysis. Those were palatal breadth at P¹P¹, P¹P¹; rostrum height, RH; C¹M¹ length; mesopterygoid fossa breadth, MFB; and greatest skull length, GSL. The DFA plots based on these five characters produced two significant functions (Figure 8). A total of 90.5% of individuals was correctly classified to their appropriate island. Three individuals from Aru were misclassified to PNG, and one individual from PNG was misclassified to Aru. Function 1, which explains 74.5% of the variation, separates the Halmahera group from both the Aru Island and PNG populations. The characters loading heavily (>6) on Function 1 were P¹P¹ and GSL (Table 6). Function 2, which explains 25.5% of the variation, separates the Halmahera group from the PNG population. The characters loading heavily (>0.6) on Function 2 were C¹M¹ and RH (Table 6).

When the DFA was run for the Aru and PNG populations and for a subset of five characters (ear

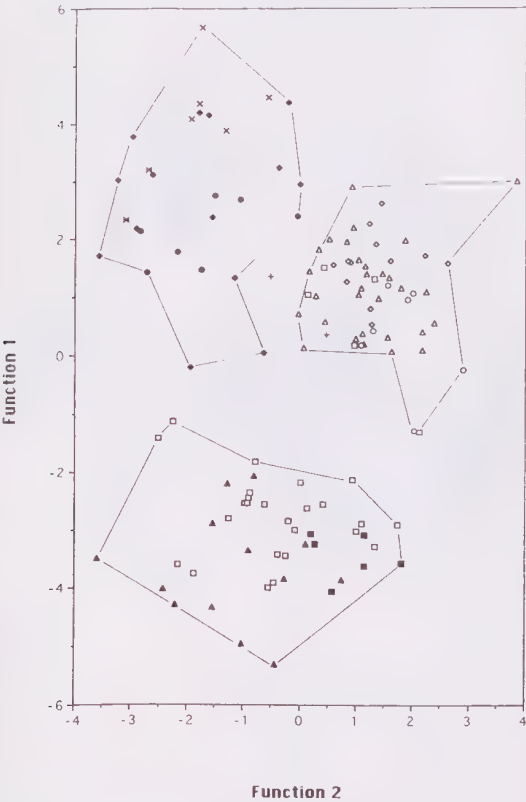


Figure 3 Canonical variate analysis on three groupings of islands, (i), Aru, Halmahera and Papua New Guinea; (ii) Kai Besar, Kai Kecil, Yamdena, and Selaru; and (iii) Seram, Ambon, Buru and Sulawesi: Banda Neira was ungrouped. The DFA plots of functions 1 and 2 were based on a selection of the same five characters as in Figure 2, with males and females combined. Symbols are as for Figure 2.

Table 4 Canonical variate function coefficients from DFA between the population of *Nyctimene cephalotes aplini* from Sulawesi and the combined populations of *N. c. cephalotes* from Seram, Ambon and Buru. Standardised values, followed by (in brackets) unstandardised values, for skull and dental characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
CBL	1.9328 (3.3396)
C'M'	-1.3704 (-3.4858)
M'M'	0.6323 (2.1542)
RH	-0.4987 (-1.5196)
PIF	-0.4524 (-0.9386)
Constant	-58.3252

length, EAR; rostrum height, RH; rostrum length, RL; C'M' length and interorbital breadth, IOB), the function extracted was highly significant with 94.9% of individuals correctly classified to their appropriate population (Figure 9). Only two Aru individuals were misclassified to the PNG group. The characters loading heaviest (>0.6) on this function were C'M' and RH (Table 7).

Summary of multivariate analyses

The above DFA supports the view that the recently described taxon *keasti* is equally distinct from both *N. albiventer* and *N. cephalotes* and should be treated as a species. Further, it shows that the Tanimbar populations, rather than being referred to *N. cephalotes* as indicated by Andersen (1912) and Hill in Corbet and Hill (1992), are more closely allied to *N. keasti*.

The Sulawesi populations referred to *N. cephalotes* are distinct from Maluku population of the species and are identified as a subspecies of *N. cephalotes*.

The species *N. cephalotes*, *N. keasti* and *N. albiventer* are rediagnosed for the study region and the Sulawesi and Tanimbar forms described as new

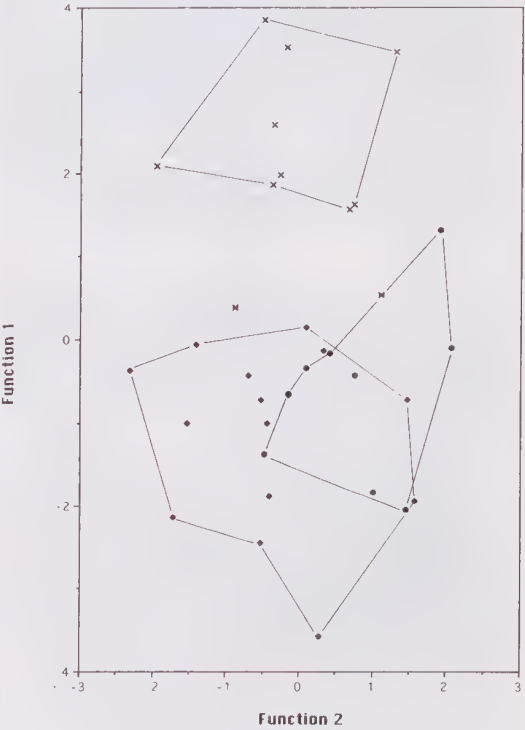


Figure 4 Canonical variate analysis among three island populations of *Nyctimene cephalotes* (Seram, Ambon and Sulawesi) with the Buru population ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five skull characters with males and females combined. Symbols as for Figure 2.

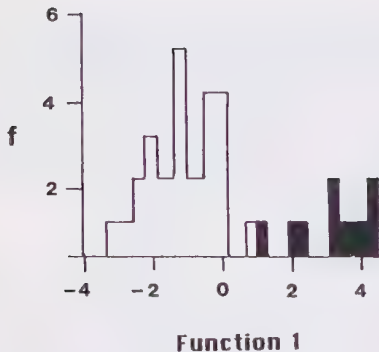


Figure 5 Canonical variate analysis between the Sulawesi population (*Nyctimene cephalotes aplini* subsp. nov.) (■) and those of the group of Seram, Ambon and Buru (*N. c. cephalotes*) (□). The histogram for function 1 was based on a selection of five skull characters, with males and females combined.

subspecies below.

The Aru form, is still phenetically close to the Papua New Guinea form, but is more differentiated morphologically from the Papua New Guinea form than was thought to be the case in Kitchener *et al.* (1993). Its subspecific status is not determined. Within the island groups of Tanimbar and Kai there has been considerable morphological differentiation between populations of subspecies of *N. keasti* inhabiting different islands. This has occurred to a lesser extent also between the Ambon and Seram populations of *N. c. cephalotes*.

SYSTEMATICS

Nyctimene cephalotes (Pallas, 1767)

Diagnosis

Nyctimene cephalotes differs from *Nyctimene*

Table 5 Canonical variate function coefficients from DFA between populations of *Nyctimene keasti* from the Kai Islands and *N. k. tozeri* from the Tanimbar Islands. Standardised values, followed by (in brackets) unstandardised values, for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
P ⁴ P ⁴	0.6922 (3.9545)
FA	-0.7606 (-1.9787)
BB	0.7532 (2.5839)
POB	-0.4283 (-1.0462)
PIF	0.3125 (0.2625)
Constant	-40.5598

Table 6 Canonical variate function coefficients from DFA between populations of *Nyctimene albiventer*, *N. a. albiventer*, *N. a. papuanus* and *N. a.* subsp. indet. from Halmahera group, and Papua New Guinea and Aru, respectively. Standardised values, followed by (in brackets) unstandardised values, for skull and dental characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1	FUNCTION 2
P ⁴ P ⁴	0.7335 (3.0491)	0.4262 (1.7717)
C ¹ M ¹	0.1907 (0.7626)	-0.9287 (-3.7137)
RH	-0.2628 (-0.8189)	0.8977 (-2.7979)
MFW	-0.5806 (-2.3344)	0.1779 (0.7151)
GSL	0.6701 (1.0692)	0.1438 (0.2295)
Constant	-35.8486	-3.3963
Variation explained (%)	74.5	25.5

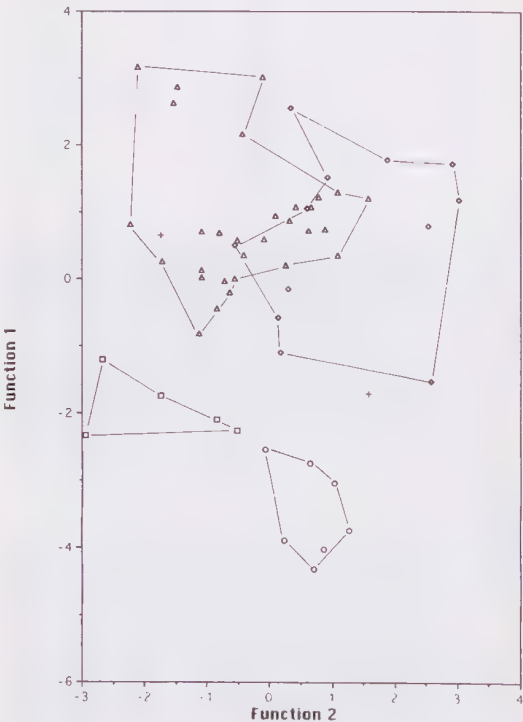


Figure 6 Canonical variate analysis among four island populations of *Nyctimene keasti*: Kai Besar, Kai Kecil (*N. k. keasti*), Selaru and Yamdena (*N. k. tozeri* subsp. nov.). The Banda Neira population was ungrouped. The DFA plots of functions 1 and 2 were based on a selection of five skull, dentary and external body characters, with males and females combined. Symbols as for Figure 2.

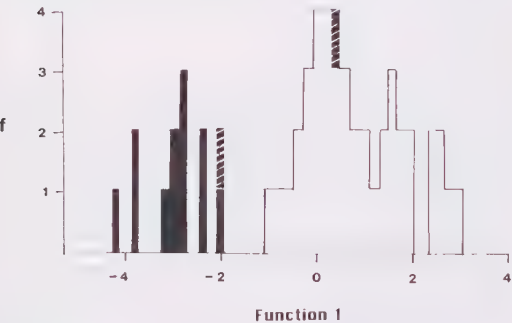


Figure 7 Canonical variate analysis between *Nyctimene keasti* populations from the Kai Island group (Kai Besar and Kai Kecil) (*N. k. keasti*) (■) and the Tanimbar Island group (Selaru and Yamdena) (*N. k. tozeri* subsp. nov.) (□). The Banda Neira population was ungrouped (▨). The histogram for Function 1 was based on a selection of five characters (skull, dentary and external body), with males and females combined.

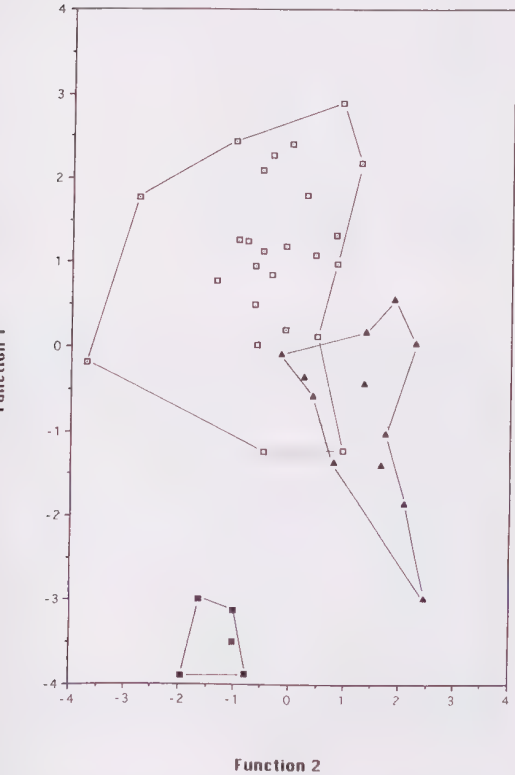


Figure 8 Canonical variate analysis between *Nyctimene albiventer* populations from the Halmahera island group (Halmahera, Morotai and Ternate) (*N. a. albiventer*), Aru (*N. a. subsp. indet.*) and Papua New Guinea (*N. a. papuanus*). The DFA plots of functions 1 and 2 were based on a selection of 5 characters (skull and dental), with males and females combined. Symbols as for Figure 2.

Table 7 Canonical variate function coefficients from DFA between populations of *Nyctimene albiventer* from Aru islands and Papua New Guinea. Standardised values, followed by (in brackets) unstandardised values for skull, dental and external body characters. For explanation of character codes see Materials and Methods section.

CHARACTER	FUNCTION 1
C'M'	0.7909 (3.0302)
RH	-0.6888 (-2.1155)
EAR	0.5633 (0.6949)
RL	0.4382 (1.6215)
IOB	-0.4345 (-1.4417)
Constant	-23.1370

albiventer by averaging larger in all measurements (Table 1). Incisive foramen to posterior palatal length shorter relative to postorbital breadth (Figure 10); C_1M_2 length generally longer relative to M^1M^1 length (Figure 11); and forearm longer relative to ear length (Figure 12). Female dorsum paler than that of males.

It differs from *Nyctimene keasti* by averaging larger in all measurements except for cranial height (Table 1). Condylbasal length generally longer relative to both rostrum height, interorbital breadth and cranial height (Figure 13A,B,C, respectively); and forearm longer relative to ear length (Figure 12).

Nyctimene cephalotes aplini Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense Number MZB 15903; adult male; weight 46 g; carcass fixed in 10% formalin and preserved in 75% ethanol; skull and mandibles separate; collected by Drs Augustine Suyanto on 28 July 1990.

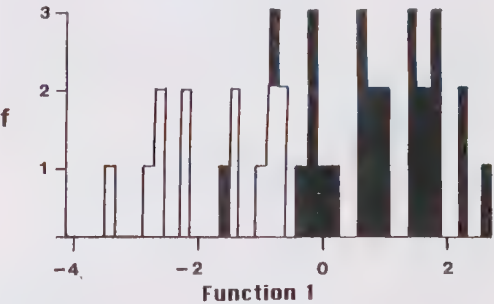


Figure 9 Canonical variate analysis between two populations of *Nyctimene albiventer*: Aru (*N. a. aruensis* subsp. nov.) (■) and Papua New Guinea (*N. a. papuanus*) (□). The histogram for function 1 was based on a selection of five characters (skull, dental and external body), with males and females combined.

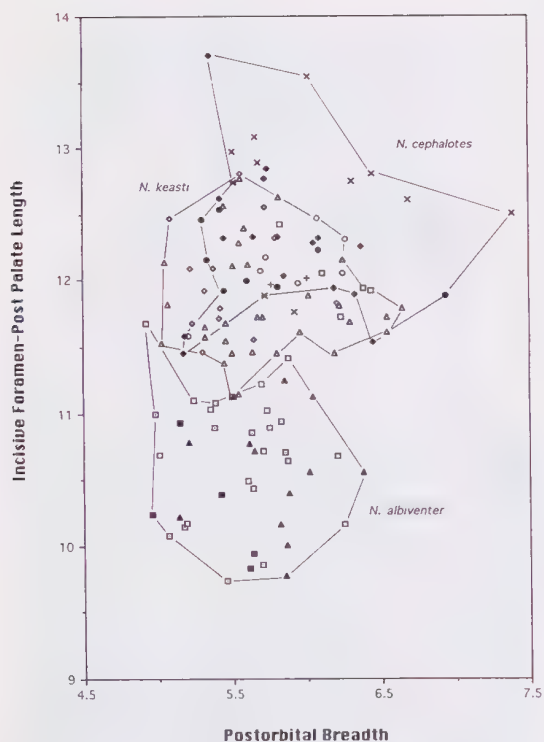


Figure 10 Plot of incisive foramen to posterior palate length *versus* postorbital breadth for all island populations of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

Paratypes

Tomado, Lake Lindu area Central Sulawesi, WAM M27659 A ♀, skin and skull; Soroako, Sulawesi Selatan, WAM M27676 A ♀, skin and skull; WAM M33145, near Bontobonto, Sulawesi Selatan (c. 5°07'S, 119°39'E), A ♀, spirit carcass and skull; Maros, Sulawesi Selatan (c. 4°59'S, 119°35'E), WAM (M33146, M33207), 2 ♂♂ skin and skull, WAM (M33208, M33210–12), 4 ♂♂, spirit carcass and skull.

Type locality

Maros, Sulawesi Selatan (= S. Sulawesi) (c. 4°59', 119°35'E), altitude c. 50 m; mist-netted.

Diagnosis

Nyctimene cephalotes aplini differs from *N. c. cephalotes* in averaging larger in all skull, mandible and external measurements; in some it is absolutely larger (Table 1). Condylobasal length greater relative to both mesopterygoid fossa breadth, MFB, and C¹M¹ length (Figures 14A,B, respectively); and zygomatic width greater relative to MFB (Figure 15).

Description

Skull, dentary and dentition

Large skull with greatest length 31.7 ± 0.47 , broad zygomatic width 21.4 ± 0.48 , palate long and broad both anteriorly, with C¹C¹ breadth 5.8 ± 0.27 , and posteriorly, with M¹M¹ breadth 9.6 ± 0.19 ; rostrum short, nasal dorsal surface almost horizontal, occasionally with dorsal distal inclination; rostrum high; premaxillary part of nares terminates directly above incisors or projects slightly anterior to them; braincase typical of *N. cephalotes* with cranium inflated to maximum height at junction of strong sagittal and weak postorbital crests; postorbital breadth large; usually deeply basined and opens anteriorly into deep frontal sulcus; frontals converging slightly posteriorly; sagittal and lambdoidal crests moderately high; incisive foramen subcircular, reach posteriorly almost to line joining P²P² anterior face; posterior palate extends well beyond M¹, its margin a broad U shape; basi- and presphenoid median ridge prominent; pterygoid process low and slightly curved ventrally and laterally.

Upper tooth row slightly curved; upper incisors in contact, sited close to line joining C¹C¹

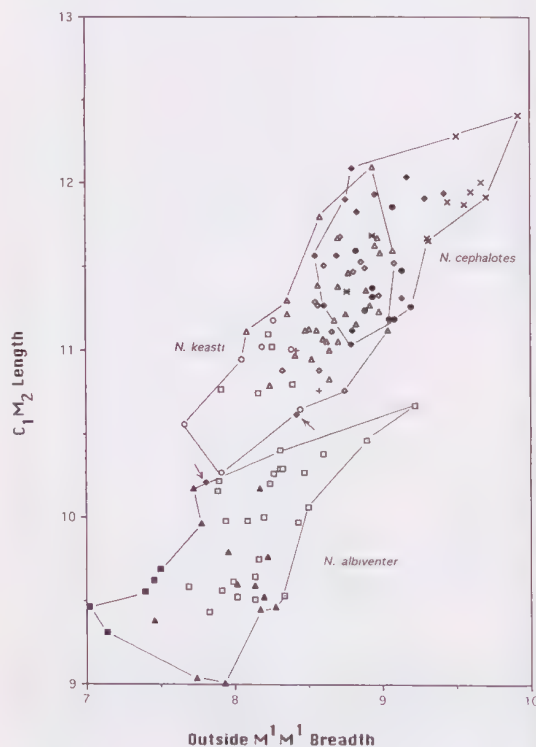


Figure 11 Plot of C₁M₂ length *versus* outside M¹M¹ breadth for all island population of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

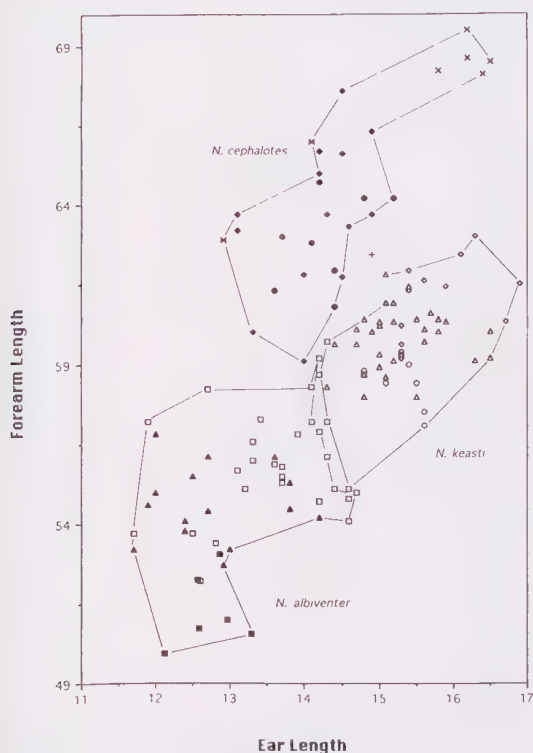


Figure 12 Plot of forearm length *versus* ear length for all island populations of *Nyctimene* studied. Males and females combined. Symbols as for Figure 2.

anteriormost face, not in contact with C_1 ; C_1 prominent cusp with gentle lingual ridge connecting to lingual and posterior cingulum, lingual cingulum occasionally with posterolingual cusplet; C_1 with moderate secondary labial cusp on posterolabial ridge, this cusp not apparent in specimens with worn teeth; P^2 subcircular, buccal area half to three-quarters that of incisors, widely spaced between C_1 and P^3 ; P^3 occlusal view suboval, with prominent labial cusp and much lower separate lingual cusp; posterior basal shelf well defined and forms slight basin, occlusal area slightly larger than P^4 ; P^4 occlusal view subrectangular with posterolingual salient from basal shelf; labial cusp lower than that of P^3 , lingual cusp less clearly defined than that of P^3 , with longer posterior ridge that reaches almost to posterolingual edge of posterior basal shelf, lingual cusp closer in height to labial cusp than in P^3 ; M^1 subrectangular, labial cusp low and only slightly taller than lingual cusp, posterior basal shelf definition similar to that of P^4 ; C_1 not in contact with each other or with P^2 ; P^2 suboval, slightly taller than C_1 cingulum; P^3 with tall labial cusp with gently sloping anterior and posterior flanges

approximately in line of tooththrow, shorter labial cusp distinct; P^4 considerably shorter than P^3 , labial cusp taller than lingual cusp but less so than in P^3 , these cusps connected by commissure that arcs around anterior face of tooth; M^1 longer and narrower than P^4 but with both labial and lingual cusps much reduced on those of P^4 ; M^2 small, about half occlusal area of M^1 . M^1 posterior shelf slightly larger than that of P^3 and P^4 .

Externals (measurements of ethanol preserved specimens followed by, in square brackets, 'cabinet' skin specimens).

Large body and ears. For example, forearm long 68.6 (68.1–69.5) 5 and [70.9 (69.0–73.0) 4]; ear long 16.2 (15.8–16.5) 5 and [16.6 (15.1–18.3) 4] and tail length 25.1 (23.7–26.2) 5 and [23.3 (19.9–27.2) 4]. Wing membrane from phalanx 1 of digit 2 in all nine specimens examined.

Males and females with similar coloured pelage. Slight colour patterning on dorsum and venter: neck to lower scapular region a broad band of paler Smoke Gray to Buff Yellow, occasionally tinged with Clay Color on shoulders and behind ears; remainder of back a darker Drab with hairs in mid dorsal region c. 9 long, merges into Fawn Color to Clay Color on flanks; median central dorsal stripe from head to tail, 2–6.5 wide and Olive Brown. Basal one-third to half of dorsum hairs pale-dark Olive Brown. Forehead and face Drab to Cinnamon; chest and abdomen Straw Yellow to Buff Yellow with abdomen occasionally Smoke Gray merging to darker Grayish Olive at flanks. Uropatagia Fuscous. Spectrum Yellow spots on patagia, ears, and skin covering all digits, particularly noticeable on forearm where spots often merge to form a broad line of colour.

Distribution

Central and South Sulawesi, probably also North Sulawesi.

Etymology

Named after our colleague, Dr Ken Aplin, Western Australian Museum, who participated in the expedition to Timor Island, Nusa Tenggara Timur, and who frequently has assisted us interpret the Indo-Malay mammal fauna.

Nyctimene cephalotes cephalotes (Pallas, 1767)

Vespertilio cephalotes Pallas, 1767: 10, pls 1,2 "Moluccas".

Vespertilio cephalotes melinus Kerr, 1792: 98. Type locality restricted to Amboina by Andersen (1912).

Cephalotes pallasi Geoffroy, 1810: 107 (renaming of *cephalotes* Pallas).

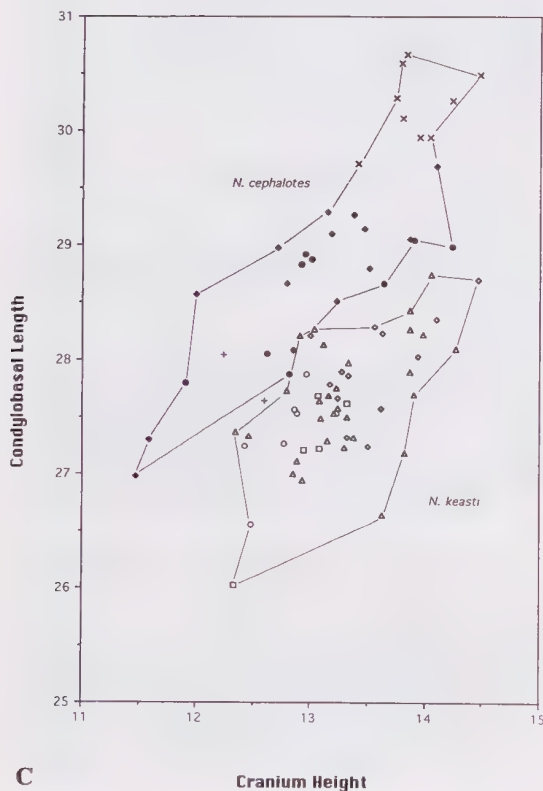
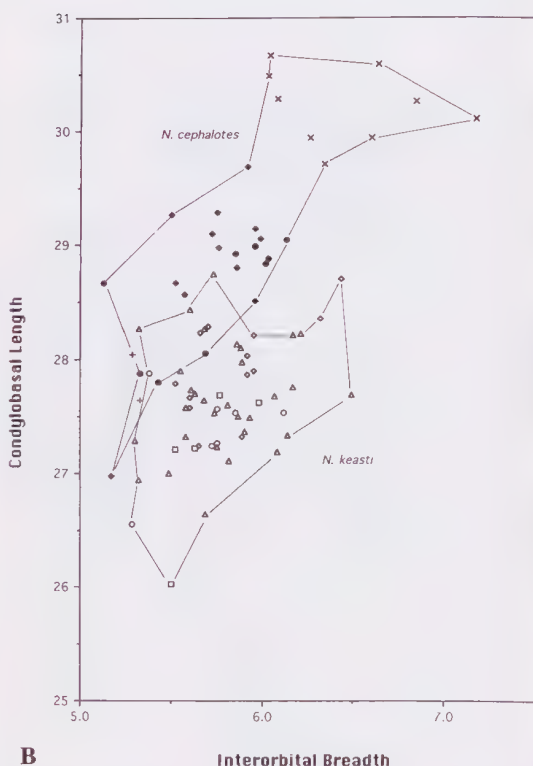
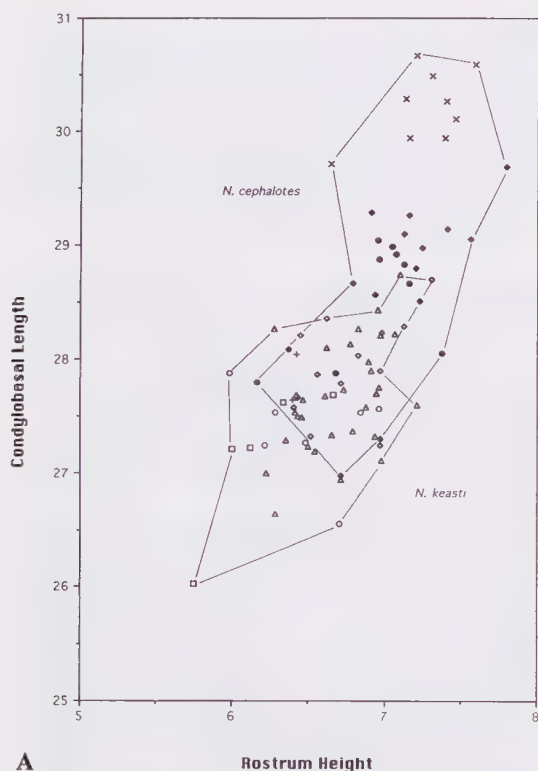


Figure 13 Plot of condylobasal length *versus* (A) rostrum height, (B) interorbital breadth and (C) cranium height for individual *Nyctimene keasti* and *N. cephalotes*. Symbols as for Figure 2.

Holotype

Andersen (1912: 707) states that "The species was described by Pallas from two female specimens from the 'Moluccas', at least one of which seems to have been in Amsterdam (in the possession of J.A. Schlosser). Whether any of the types are still in existence is unknown".

Type locality

Type locality fixed as Amboina by Andersen (1912: 707).

Specimens examined

INDONESIA

Ambon Island: Ambon, 3°41'S, 112°10'E, WAM M(38762, 38778, 38821–22, 38861, 42351, 42364) (4 ♀, 3 ♂).

Desa Amahusa, 3°41'S, 128°10'E, WAM M(43128, 43921) (1 ♀, 1 sex unknown)

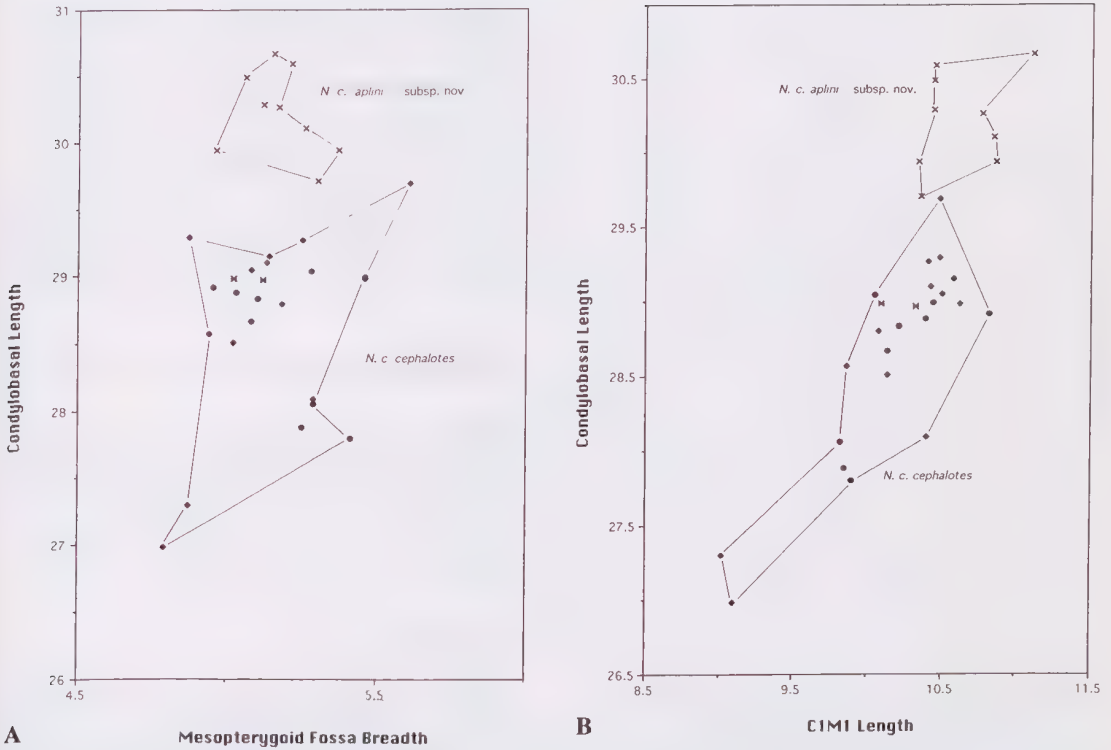


Figure 14 Plot of condyllobasal length versus (A) mesopterygoid fossa breadth and (B) C¹M¹ length for individual *Nyctimene cephalotes*. Symbols as for Figure 2.

Buru Island: S.W. Buru, c. 3°40'S, 126°30'E, WAM M(43883–84) (2 ♀ ♀).

Seram Island: Kanikeh 3°06'S, 129°28'E, WAM M(34560–3, 34565) (1 ♀, 4 ♂ ♂). Solea, 2°53'S, 129°32'E, WAM M(34548, 34550–6, 34558–9 (3 ♀ ♀, 7 ♂ ♂).

Diagnosis

Nyctimene c. cephalotes differs from *N. c. aplini* as described in the earlier diagnosis of that subspecies.

Description

Skull moderately long 30.1 ± 0.68 , narrow with braincase breadth 12.8 ± 0.37 and zygomatic width 19.8 ± 0.72 ; palate posterior margin V or sharp U shape; mesopterygoid fossa moderately wide 5.2 ± 0.20 ; C¹M¹ tooth row moderately long 10.2 ± 0.43 ; I¹ generally closely opposed to C¹, sometimes in contact with C¹; incisive foramen subcircular, small, generally not reaching posteriorly to a line joining P²–P² anterior face; frontal between postorbital process flat or only very slightly basined.

Apart from the above characteristics and generally smaller size, the shape of the skull,

dentary and dentition is very similar to *N. cephalotes aplini*.

Externals

Forearm moderately long 63.4 ± 2.07 ; ear moderately long 14.2 ± 0.61 . Wing membrane generally connected between phalanx 1 of digits 2 and 3 (46%, N = 13) but also commonly from phalanx 1 of digit 3 (29%, N = 8) and commonly from phalanx 1 of digit 2 (25%, N = 7).

Pelage

Males and females with similar coloured dorsum but females with paler head, face and ventral pelage and paler patagia. The dorsal surface of males and females predominantly Drab but tipped with Olive Brown on shoulders and patchily with Fawn Color on lumbar and lower back regions; median dorsal stripe from crown of head to base of tail Olive Brown varying in breadth from 2–5. Hairs in mid dorsal region c. 11 long, basal one-third Drab. On head and behind ears to shoulders, Clay colour in males; in females a paler Straw Yellow. On face dark Smoke Gray in males; in females a paler Smoke Gray. Ventral surface in males Cream Color on chest and abdomen with neck and flanks Buff Yellow to Buff; in females

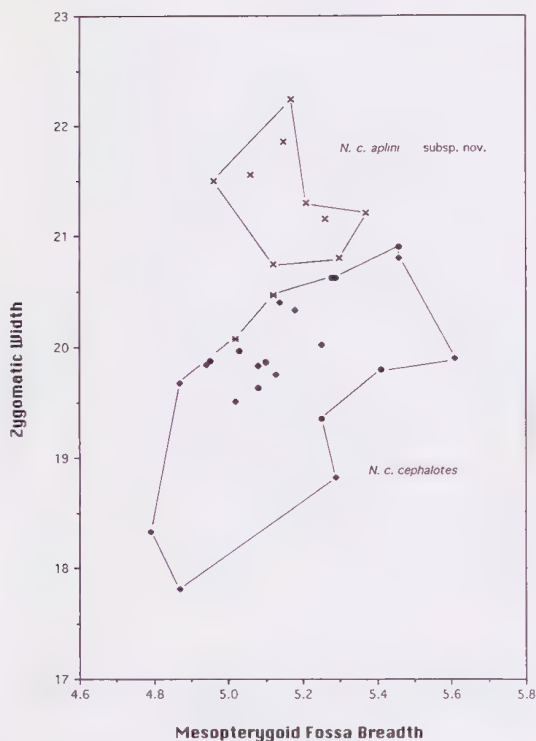


Figure 15 Plot of zygomatic width versus mesopterygoid fossa breadth for individual *Nyctimene cephalotes*. Symbols as for Figure 2.

ventral surface a uniform Cream Color. Patagia in males Olive Brown; in females a paler Fawn Color. Spots on patagia spectrum Yellow and distributed similarly to *N. cephalotes aplini*.

Distribution

Seram, Ambon and Buru Islands, Maluku Tenggara, Indonesia. It is unlikely that the *Nyctimene* from Timor Island attributed to *N. cephalotes* by Anderson (1912), Goodwin (1979) and Hill in Corbet and Hill (1992) is of that species. It is more likely to be associated with *N. keasti*.

Nyctimene keasti Kitchener, 1993

Nyctimene albiventer keasti Kitchener et al., 1993: 408–412

Diagnosis

Nyctimene keasti differs from *N. cephalotes* as described in the earlier diagnosis of *N. cephalotes*. It differs from *N. albiventer* in averaging larger in all skull, mandible and external measurements. For example, greatest skull length 29.34 (28.04–30.78)

56 v. 26.98 (24.67–28.45) 45; braincase breadth 12.64 (11.64–13.94) 56 v. 11.93 (11.10–13.06) 45; zygomatic width 19.28 (18.11–20.40) 56 v. 18.07 (16.55–19.69) 45; C¹M¹ length 9.91 (8.39–10.50) 56 v. 8.82 (8.20–9.51) 45; forearm length 59.7 (55.1–63.0) 56 v. 54.9 (49.9–59.2) 48; and ear length 15.3 (14.2–16.9) 56 v. 13.2 (11.7–14.7) 48; forearm length generally longer relative to ear length (Figure 12); incisive foramen to posterior palate length, PIF, relatively greater relative to postorbital breadth (Figure 10); C₁M₂ length greater relative to M¹M¹ width (Figure 11).

Nyctimene keasti tozeri Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense Number MZB 15904, adult male, weight 29.5 gm, carcase fixed in 10% formalin and preserved in 75% ethanol; skull and mandibles separate, liver preserved in ultrafreeze at WAM, collected by D.J. Kitchener and R.A. How on 27 April 1993.

Type locality

Lorulun (Figure 1) c. 20 km N Saumlaki, Yamdena Island, Tanimbar group; Maluku Tenggara, Indonesia (7°52'S, 131°25'E); altitude 200 m. Mist netted at c. 2m height in disturbed vine forest with the following genera of trees prominent: *Ficus*, *Erythrina*, *Podocarpus*, *Albizia* as well as 'Kenari' trees. The understory was mostly Lantana. There were numerous vines and creepers (see Kitchener and Maryanto 1994: Figure 5).

Paratypes

Yamdena Island: Desa Sifnana Omele, 7°56'S, 131°18'E, WAM 44398–401 (3♀, 1♂); Desa Lorulun (7°52'S, 131°25'E), WAM M(43776, 43782–88, 4394–95, 43798, 43801–06, 43809) (10♀, 8♂); Saumlaki, 7°59'S, 131°22'E, WAM M(43511–12, 43555–58, 43564–66, 43600) (8♀, 1♂). Selaru Island: Desa Adaut, 8°09'S, 131°08'E, WAM M(44201–05, M4408, M44300–03, M44310–11, M44316) (11♀, 2♂).

Diagnosis

Nyctimene keasti tozeri differs from *N. k. keasti* in averaging larger in all skull, mandible and external measurements, except for incisive foramen to posterior palate length (PIF) and postorbital breadth (Table 1). Palatal length between P⁴P⁴ lingual surface broader relative to both postorbital breadth and PIF (Figures 16 A,B, respectively); braincase breadth generally larger relative to postorbital breadth (Figure 17). It differs also from *N. k. keasti* in females having pelage of dorsum a similar dark Drab colour to that of males rather than females with a dorsum of Buff Yellow which is paler than the male Fawn color dorsum.

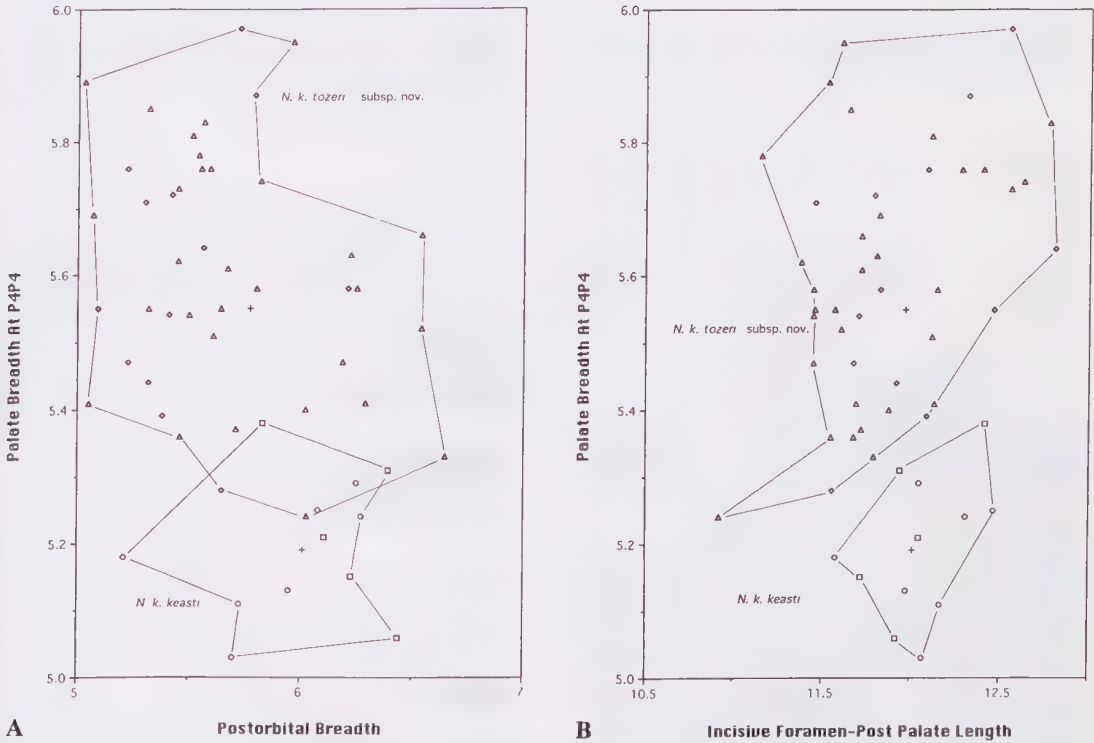


Figure 16 Plot of palate breadth at P4p4 versus (A) postorbital breadth and (B) incisive foramen to posterior palate length for individual *Nyctimene keasti*. Symbols as for Figure 2.

Description

Skull, dentary and dentition

Intermediate sized skull with greatest length 29.5 ± 0.56 ; zygomatic width 19.4 ± 0.45 ; braincase breadth 12.7 ± 0.29 and C'M1 length 10.0 ± 0.34 (Table 1). Very similar in shape to *Nyctimene cephalotes aplini* except that the junction of the postorbital ridges and sagittal crest closer to postorbital process base and frontal area immediately anterior to this junction is less basined than is the case in *N. c. aplini*.

Externals

Forearm moderately long 60.1 ± 1.12 ; ear moderately long 15.4 ± 0.60 . wing membrane usually attached to pes between phalanx 1 of digits 2 and 3 (56%, $N=25$); also commonly attached to phalanx 1 of digit 2 (16%, $N=7$), and phalanx 1 of digit 3 (27%, $N=12$) and rarely to between digits 3 and 4 at level of phalanx 1 (2%, $N=1$).

Pelage and patagia colouration very similar to *N. c. cephalotes*. Namely male and female dorsal surface of similar colour but with females having a paler head, face and ventral surface.

Distribution

Yamdena, Salaru and Larat islands, Tanimbar group, Maluku Tenggara, Indonesia.

Etymology

Named after Mr Tom Tozer, a distinguished retired gentleman, who for many years provided honorary assistance in the mammal section, Western Australian Museum, primarily with the curation of the Indonesian collection.

Referred specimens

The two specimens from Banda Neira Island, Band Group were included in the paratype series of *Nyctimene albiventer keasti* Kitchener, 1993 in Kitchener *et al.* (1993). These two specimens are treated as unallocated in the preceeding multivariate analysis because they are not readily attributable to either *N. cephalotes* or *N. keasti*. They may represent a distinct form of *Nyctimene* but if referable to a recognisable form of *keasti*, they are clearly associated with *N. k. tozeri*. The taxonomic relationships of the Banda Island form will be clarified when more specimens become available for study.

The specimen WAM M34549, adult male, alcohol and skull specimen, collected from Solea, Seram, was included in all the preceding statistical analysis as an unallocated specimen. It has a short forearm (58.0) and skull and external measurements similar to *N. keasti tozeri*. It was clearly allocated to this taxon in the DFA.

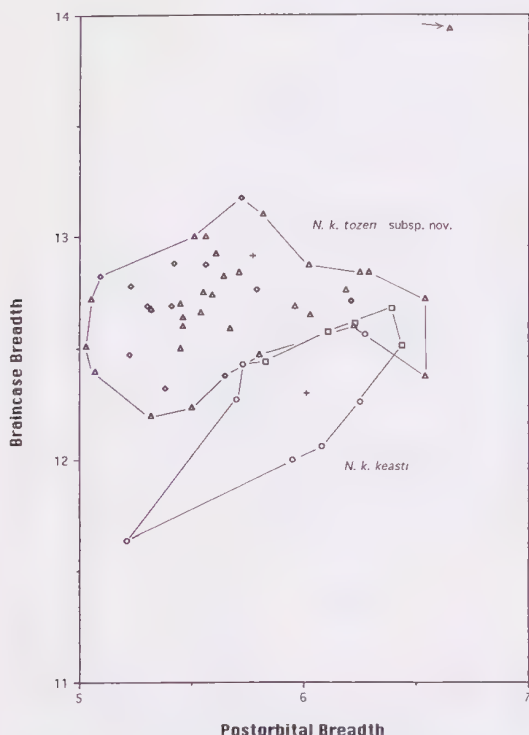


Figure 17 Plot of braincase breadth versus postorbital breadth for individual *Nyctimene keasti*. Symbols as for Figure 2.

Nyctimene albiventer albiventer (Gray, 1863)

Cynopterus albiventer Gray, 1863: 261–63

Holotype

The Natural History Museum, London Number BMNH 62.10.21.5; adult, 'cabinet' skin and skull, collected by Dr. A.R. Wallace in 1861.

Type locality

Morotai Island, Maluku Utara, Indonesia (c. 2°30'N, 128°30'E)

Specimens examined

Listed in Kitchener *et al.* (1993)

Diagnosis

Nyctimene albiventer albiventer differs from *N. a. papuanus* in averaging smaller in all measurements except rostrum length (see Kitchener *et al.* 1993: Table 1). Forearm length generally smaller relative to ear length (Kitchener *et al.* 1993: Fig 4) and palatal breadth at P⁴P⁴ generally smaller relative to rostrum length (Kitchener *et al.* 1993: Figure 3b).

If differs from *N. albiventer* subsp. indet. from Aru Island in averaging smaller in all measurements, except rostrum length, mesopterygoid fossa breadth and snout to vent

length (see Kitchener *et al.* 1993: Table 1). P⁴P⁴ breadth also smaller relative to greatest skull length (see Kitchener *et al.* 1993: Figure 3a); and ear length longer relative to forearm length (see Kitchener *et al.* 1993: Figure 4).

Description

A small subspecies of *N. albiventer* with greatest skull length 25.68 ± 0.60 and forearm length 51.2 ± 1.2 (see Kitchener *et al.* 1993, Table 1). The overall shape of skull, dentary, and dentition similar to *N. cephalotes aplini*. Its pelage and colour are similar to that described earlier for *N. c. cephalotes*. Wing membrane attached to pes on phalanx 1 of digit 3 (Andersen 1912: 701).

Distribution

Morotai, Gilolo, Ternate and Goal area, N. Halmahera Island.

Nyctimene albiventer papuanus K. Andersen, 1910

Nyctimene papuanus K. Andersen, 1910: 621.

Holotype

The Natural History Museum, London Number

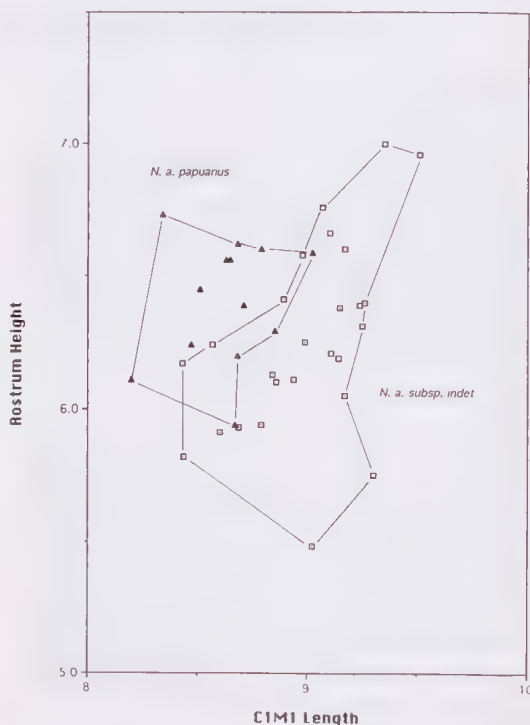


Figure 18 Plot of rostrum height versus C'M1 length for individual *Nyctimene albiventer* subsp. indet. and *N. a. papuanus*. Symbols as for Figure 2.

BMNH 99.12.3.2, adult male, 'cabinet' skin, skull and mandibles separate, collected by A.S. Meek on 19 March 1899.

Type locality

Milne Bay, Papua New Guinea, (ca. 10°20'S, 150°30'E)

Species examined

Listed in Kitchener *et al.* (1993)

Diagnosis

Nyctimene albiventer papuanus differs from *N. a. albiventer* as described in the earlier diagnosis of that species.

It differs from *N. albiventer* subsp. indet. from Aru in having skull, tooth row and external measurements that generally average smaller. Rostrum height generally less relative to C¹M¹ length (Figure 18).

Description

Intermediate in overall skull, dentary, dental and external characters between *N. a. keasti* and *N. a. albiventer* (for measurements see Kitchener *et al.* 1993: Table 1).

Pelage colour similar to earlier *N. c. cephalotes* description. Wing membrane attached equally commonly to phalanx 1 of digit 2 (47%, N = 7) or at this level between digits 2 and 3 (53%, N = 8). Andersen (1912) stated that in the 14 specimens of *papuanus* he examined, this membrane was usually attached to phalanx 1 of digit 2 (79%, N = 11), and occasionally between digits 2 and 3 at level of phalanx 1 (14%, N=2) and on phalanx 1 of digit 3 (7%, N = 1).

Distribution

Irian Jaya: Andai, Skiu. Papua New Guinea: Eaga, Stephansort, S. Coast, Milne Bay; Olsbip, Upper Fly River; near Wewak, E. Sepik; near Baku, Gogol Valley, Madang; Lobota Cave, and Buso, Morobe. Admiralty Island and Bismark Archipelago (Andersen 1912, Hill 1983).

Nyctimene albiventer subsp. indet.

Diagnosis

This is a large form of *N. albiventer* which has the overall shape of the skull, dentary, dentition and colour of pelage of *N. a. papuanus* (for measurements see Kitchener *et al.* 1993: Table 1). It may be diagnosed against *N. a. albiventer* and *N. a. papuanus* as described in the earlier diagnoses of those subspecies.

The wing membrane attaches to the pes usually

on phalanx 1 of digit 2 (62%, N = 10) but also commonly at level on phalanx between digits 2 and 3 (25%, N = 4), or on phalanx 1 of digit 3 (13%, N = 2).

Distribution

Wokam Island, but probably all other islands in the Aru group.

Specimens examined

Listed in Kitchener *et al.* (1993)

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of Mr J. Bannister, previous Director, Western Australian Museum and the current Director Mr A. Reeves; Drs M. Amir, Director, Balitbang Zoologi (LIPI); and the Director of the Indonesian Department responsible for the conservation of wildlife in Maluku Tenggara, Ir. J. Rustandi, who provided us with assistance in the field, as did a number of his staff. To our colleagues Dr Ric How and Mr Ron Johnstone, Western Australian Museum, and Ir Ibnu Maryanto, Museum Zoologicum Bogoriense, who participated in the exhausting field work, we extend our thanks for both their effort and companionship. Dr Ken Aplin and Dr R.A. How, Western Australian Museum, kindly reviewed the manuscript. We are grateful to Dr Tim Flannery, Australian Museum for the loan of specimens of *Nyctimene* from Ternate, Morotai and Halmahera islands. Expedition costs were defrayed by grants to D. Kitchener from: National Geographic Society, Washington and Australian National Parks and Wildlife Service, Canberra. Some expenses were borne personally. Garuda Indonesia kindly defrayed freight costs of the expeditions. Mr C. Keast and Mrs N. Cooper, Western Australian Museum removed and cleaned the skulls. Mrs N. Cooper, Western Australian Museum, ran the computer analyses. Mrs S. Dalton, Western Australian Museum, typed the manuscript.

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Manuscript received 10 January 1994; accepted 15 July 1994.

A theropod dinosaur bone from the Late Cretaceous Molecap Greensand, Western Australia

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Abstract – A proximal pedal phalanx from a theropod dinosaur is recorded from the Late Cretaceous Molecap Greensand, at Gingin, Western Australia. It is only the second record of a Late Cretaceous dinosaur from Australia, and the first dinosaur bone recovered from the Perth Basin.

INTRODUCTION

Dinosaur remains are extremely rare in Western Australia. Only two bones have been previously recorded, a sauropod caudal vertebra from the Middle Jurassic Colalura Sandstone exposed at Bringo Cutting, near Geraldton, and a possible theropod humerus from the Late Cretaceous (late Maastrichtian) Miria Formation in the Giralia Range, south of Exmouth Gulf (Long 1992). In July 1992 a University of Western Australia Geology Department second year field excursion to the Molecap Quarry, at Gingin, discovered the third dinosaur bone from the state. The specimen, a small pedal phalanx, was found by student Michael Green and donated to the Western Australian Museum. The bone (WAM 92.7.1, Figure 1, 2 E–H) was found *in situ* in the Molecap Greensand at a height of about 2 metres above the quarry floor in the western face of the quarry. The age of the Molecap Greensand has been assessed as ranging from Cenomanian to lower Turonian (Shafik 1990) to possibly Santonian (McWhae *et al.* 1958). To date the only other vertebrate remains recovered from the Molecap Greensand are chondrichthyan and teleost teeth, three mosasaur paddle bones (Lundelius and Warne 1960), and isolated plesiosaur and ichthyosaur bones and teeth (McNamara *et al.* 1993; Long 1993).

The only other bones of theropod dinosaurs described from Australia are all of Early Cretaceous age. An isolated theropod claw from Cape Patterson, southern Victoria, was described by Woodward (1906), and a caudal vertebra from Lightning Ridge was named as *Walgettosuchus woodwardi* by Von Huene (1932), although it is now regarded as a *nomen dubium* (Molnar 1991). A partial tibia and an isolated phalanx from Andamooka, South Australia, were identified as belonging to a new slender theropod called *Kakuru kujani* (Molnar and Pledge 1980). The Victorian

outcrops of the Strzelecki and Otway Groups include an astragalus of *Allosaurus* sp. (Molnar *et al.* 1981), and undescribed vertebrae, jaw and limb bones from theropods, including ornithomimosaurs and a possible oviraptorid (Rich 1993; Rich *et al.* 1991, Rich and Vickers-Rich 1994).

The comparison made between the Gingin theropod and *Allosaurus fragilis* shown in Figure 2 is not to suggest that the Gingin specimen is here identified as *Allosaurus*, only to make the point that the specimen is a theropod with very close resemblances to *Allosaurus*. It is beyond the scope of this paper to compare phalangeal proportions of the known theropod dinosaurs with the Gingin specimen, only to record the specimen and make some general observations and comparisons.

DESCRIPTION OF THE SPECIMEN

The Gingin phalanx (WAM 92.7.1, Figure 1) is 40.8 mm in length, 25.7 mm proximal depth, 26.2 mm proximal width, 20.8 mm distal depth and 24.4 mm in distal width. The asymmetry of the distal articular condyles indicates it is from the left pes. The ventral surface shows the presence of a thickened platform of rugose bone close to the posteromedial corner (the flexor tubercle, shown arrowed in Figure 2 B, F) and the posterolateral corner has a slightly concave area of bone. The proximal face is relatively flat with only weak development of the articular ridges which received the distal face of the fourth metatarsal. In lateral view the ventral margin of the shaft of the bone is strongly concave, and the articular condyles of the distal end are well rounded and stand out prominently from the neck of the shaft. The distal end of the phalanx has well-defined, quite large collateral ligament fossae on each side.

The bone is well preserved and its characteristic proportions indicate that it is a pedal phalanx of a

theropod dinosaur by direct comparison with that of *Allosaurus fragilis* (Madsen 1976) and other theropods (casts and material examined by the author include *Tyrannosaurus*, *Tarbosaurus*, *Albertosaurus*, *Deinonychus*, *Allosaurus* and isolated ornithomimosaur pedal phalanges from the Judith River Formation, Alberta) differing from *A. fragilis* only by its smaller size and slight proportional differences, such as the depth of the proximal end (Figure 1 A, E). The phalanges of the manus in *Allosaurus* are all much narrower with more slender shafts than observed in the Gingin bone. In addition, a cast of the bone was shown to various dinosaur experts (Dr Philip Currie, Dr Peter Dodson, Mr Gregory Paul) in the U.S.A. at the Dino Fest Conference (Indianapolis, March 1994) who all commented that it appeared to be "an indeterminate theropod pedal phalange" bone.

In general the phalanges of ornithopods reflect their broader feet proportions in having wider phalanges with flatter dorsal and ventral surfaces. Direct comparisons were made with casts of *Muttaburrasaurus*, *Hypsilophodon*, *Sauroplophus*, *Corythosaurus* and *Iguanodon*. Only the fourth digit proximal phalanx in *Allosaurus* has the same proportions as the Gingin bone in that the proximal face is relatively triangular in outline, much deeper than the distal end, and lacks a distinct vertical median crest (Madsen 1976, figs 54, 55).

The size of the Gingin bone is about half the length of the equivalent element in *Gorgosaurus libratus* (WA Museum cast of 1933 Sternberg specimen) and approximately half the size of that in *Allosaurus fragilis*. Based on the adult sizes of these carnosaurs it is estimated that the Gingin theropod may have been about 4 metres maximum length.



Figure 1 Theropod pedal phalanx, proximal element of fourth digit, left side. WAM 92.7.1.Molecap Greensand (Late Cretaceous), Molecap Quarry, Gingin, Western Australia. Specimens shown in A, dorsal; B, ventral; C, left lateral; D, distal and E, proximal views.

DISCUSSION

In its robust nature the specimen differs from the slender phalanges of advanced theropods like dromaeosaurids, oviraptorosaurids, troodontids and

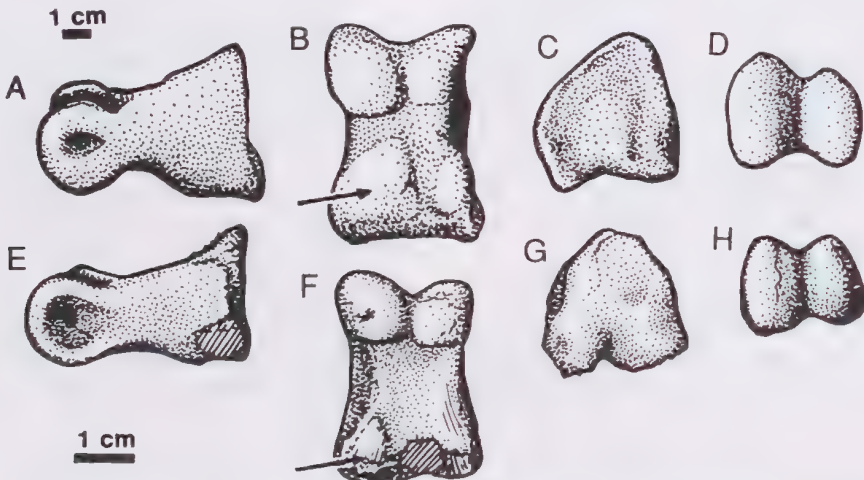


Figure 2 Comparison between the left fourth pedal proximal phalanx in *Allosaurus fragilis* (A-D) and the Gingin theropod (E-H). A, E, lateral views; B, F, ventral views, arrow points to flexor tubercle; C, G, proximal face; D, H, distal view of articular condyles. A-D after Madsen (1976).

ornithomimosaurs (Barsbold *et al.* 1990; Currie 1990; Barsbold and Osmolska 1990; Molnar *et al.* 1990; Osmolska and Barsbold 1990; Ostrom 1990) and appears to match most closely the generalised form of a carnosaur proximal pedal phalanx. Comparison with Late Cretaceous tyrannosaurids is precluded largely by the absence of published information on the phalanges, although a cast of the Sternberg skeleton of *Gorgosaurus libratus* from Alberta in the Western Australian Museum, and the author's examination of the American Museum of Natural History *Tyrannosaurus rex* skeleton, and of the mounted skeleton of *Tarbosaurus bataar* (touring Australia in 1993–1995 as part of The Great Russian Dinosaurs Exhibition) permits some observations to be noted.

In *Gorgosaurus* the fourth digit proximal phalanx is much more elongated and the ventral margin of the shaft is more strongly concave than for the Gingin specimen. In *Tyrannosaurus rex* and *Tarbosaurus bataar* the fourth proximal phalanx is of quite robust, short proportions and is comparable in general form with that of *Allosaurus* or the Gingin specimen, differing principally by their larger size.

Finally, one other theropod phalanx has been described from Australia, an isolated element from Andamooka (Early Cretaceous, Aptian Marree Formation) referred to *Kukuru kujani* by Molnar and Pledge (1980). This specimen differs from the Gingin bone by its extremely slender shape with the distal and proximal faces of the bone being of approximately equal depth. Comparison with abelisaurids is difficult as few have shown preservation of the feet. The problematical theropod *Noasaurus*, from the Late Cretaceous of Argentina has one of the phalanges preserved. It is unusual in having deep flexor pits on the ventral surface rather than a flexor tubercle, and differs from the Gingin bone in this feature (Bonaparte and Powell 1980).

In summary, the small phalanx from the Molecap Greensand (WAM 92.7.1) is here referred to an indeterminate theropod dinosaur, most likely a member of the Carnosauria having similarities to the Allosauridae. The latest recorded members of this family are Aptian-Albian, from Australia (Molnar *et al.* 1981), North America and Mongolia (Molnar *et al.* 1990). At this stage a determination to generic level is not possible until more theropod pes material is discovered.

ACKNOWLEDGEMENTS

My sincere thanks must go to Michael Green for finding and donating the specimen to the W.A. Museum, and to Ralph Molnar for his helpful criticism of the draft manuscript. The organisers of the Dino Fest Conference held in Indianapolis,

March 24–27th 1994, are thanked for funds allowing me to travel to the USA and examine dinosaur material in the American Museum of Natural History (New York), and the Field Museum, Chicago. Thanks to Kris Brimmell for the photography of the specimen.

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Manuscript received 11 May 1994; accepted 15 August 1994.

Small *Pteropus* (Chiroptera: Pteropodidae) from Timor and surrounding islands, Indonesia

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Abstract – A series of 10 adult *Pteropus* specimens collected in West Timor in 1929 are described as a new subspecies, *Pteropus lombocensis salottii* Kitchener. These specimens are compared using univariate and multivariate statistical analysis, principally of skull and dentary characters, with other subspecies of *P. lombocensis* and with both *P. griseus* and *P. temmincki*. This is the first report of *P. lombocensis* from Timor and Komodo.

INTRODUCTION

Three species of *Pteropus* have been reported from Timor Island, Nusa Tenggara Timur, Indonesia. These are *P. vampyrus edulis* Geoffroy, 1810; *P. alecto* ? *gouldi* Peters, 1867 and *P. g. griseus* Geoffroy, 1810 (Andersen 1912, Goodwin 1979, Hill 1992 and Kitchener *et al.* 1995a). Timor is the type locality for *P. g. griseus*.

Goodwin (1979: 88) stated that the many reports of *P. temmincki* Peters, 1867 from Timor and Semaue (e.g., Dobson 1878, Andersen 1912, Schwarz 1914) are with one exception "traceable to misidentifications of specimens of *P. griseus*". The exception is the British Museum specimen BMNH 58.11.18.2, initially cited by Dobson (1878). Goodwin (1979) confirmed that this specimen was indeed *P. temmincki*. However, he stated that because it was purchased from a dealer in Holland, its provenance may be doubtful. His reason for doubt was that its occurrence on Timor would represent a "rather anomalous distribution pattern" because elsewhere it is restricted to Ambon, Buru and Seram.

Goodwin (1979) also doubted the report by Seabra (1897) of *P. pselaphon* Lay, 1829 from Timor. His examination of this Timor specimen in the Museu Bocage, Lisbon (MB296) suggested that it was in fact an immature *P. griseus*.

The Museum Zoologicum Bogoriense has a series of 10 adult *Pteropus* skulls and skins (MZB 2182, 2184, 2189–96) collected by Mrs Walsh, on 3 February 1929 from Soe, West Timor, at an altitude of 880 m and one (MZB 9208) from Komodo Island. These specimens appeared to have been overlooked by previous workers. The Timor specimens are of particular interest because they are a small bat (forearm 109–115 mm) but with pelage and skull and body dimensions allied to, but differing, from both *P. griseus* and *P. temmincki*;

they clearly do not represent the much larger *P. pselaphon*. This paper reports on an examination of the taxonomic status of these MZB specimens and compares their morphology to *P. lombocensis*, *P. griseus* and *P. temmincki*.

MATERIALS AND METHODS

Ten adult skulls and 'cabinet skins' (1♂, 9♀) in the MZB series of *Pteropus* from Timor Island (2182–97) were measured and compared with the following specimens (all currently lodged in the Western Australian Museum). *P. griseus griseus*, Panite, W. Timor Island (9°50'S, 124°29'E), 1♂, (WAM M34858); Uiasa, Semaue Island (10°10'S, 123°28'E), 2♂♂ (WAM 35592–3); Baa, Roti Island (10°46'S, 123°16'E), 4♂♂ 1♀, (WAM M35400, M35405–57, M35420); Ipokil, Wetar Island (7°50'S, 126°16'E), 1♂ (WAM M44679). *P. griseus pallidus* Temminck, 1825, Banda Neira Island (4°31'S, 129°50'E), 3♂♂ 3♀♀ 1 ? sex (WAM M42004–7, M42377, M42381, M42393). *P. temmincki temmincki*, Amboinea, Ambon Island (3°41'S, 128°10'E), 2♂♂ 1♀, (WAM M43130–31, M43900); Solea, Gunung Manusela, Seram Island (2°53'S, 129°32'E), 3♂♂, (WAM M34520–22) and *P. lombocensis lombocensis* and *P. l. heudei* listed in Kitchener *et al.* (1995a).

The measurements were recorded only from adults. These measurements were the same as those reported in Kitchener *et al.* (1995a), with two additional measurements. These were maximum diameter of the orbit and dentary coronoid height. Only forearm length was measured from the external body. This was because this was the only measurement from the skins of the MZB specimens that was comparable to the external preserved specimens. Only skull, dentary and dental measurements were used in the statistical comparison of the MZB specimens with the others.



Figure 1 Locality of specimens used in this study. *Pteropus g. griseus* (○); *P. g. pallidus* (●); *P. t. temmincki* (▼); *P. l. lombocensis* (■); *P. l. heudei* (□) and *P. l. salottii* (★).

Adult condition was judged to be when both the basioccipital/basisphenoid and basisphenoid/presphenoid sutures were fused.

The statistical procedures were as described in Kitchener *et al.* (1995a). Both sexes were combined. The stepwise canonical variate (discriminant function) analysis was initially run for all 20 skull characters for islands separately and islands grouped. The DFA was then run for a subset of 5 of these characters on the grouped populations. This subset was selected to minimise Wilk's lambda. This was because the full set of characters exceeded the sample size of the smallest island group examined. Because the DFA plots using the subset of characters were very similar to those when all characters were employed in the DFA, only the analysis carried out with the reduced set of characters are presented below.

RESULTS

Discriminant Function Analysis

The preliminary analysis using all 20 characters clearly placed the single Komodo Island specimen with *Pteropus l. heudei*.

All groups/taxa

A DFA was run based on 6 taxon/groups (the

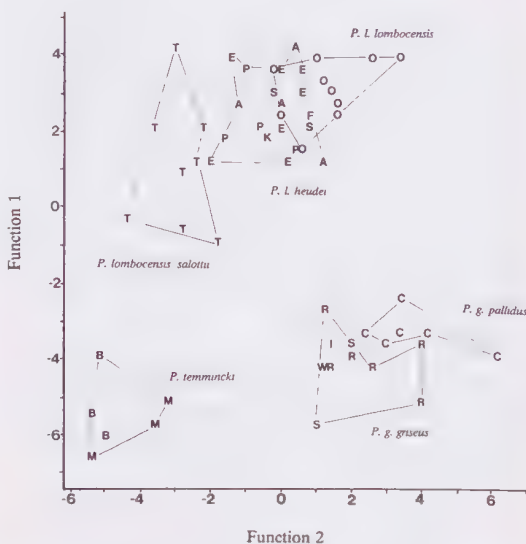


Figure 2 Plot of Functions 1 and 2 from DFA based on six taxa [*Pteropus l. salottii* (Timor, T); *P. l. lombocensis* (Lombok, O); *P. l. heudei* (Flores, F; Lembata, E; Pantar, P; Alor, A; and Komodo, K); *P. g. griseus* (Wetar, W; Timor, I; Semau, S; and Roti, R); *P. g. pallidus* (Banda Neira, C); and *P. t. temmincki* (Ambon, B; Seram, S)] and five selected skull characters.

Table 1 Canonical Variate Function Coefficients from DFA between six taxon (*Pteropus lombocensis* – Timor; *P. l. lombocensis*; *P. l. heudei*; *P. g. griseus*; *P. griseus pallidus* and *P. t. temmincki*) and based on five cranial characters (see text). Standardised values followed by (in brackets) unstandardised values.

Character	Function 1	Function 2
P ³ breadth	−0.6906 (−1.2756)	0.5497 (1.0153)
Rostrum length	0.7794 (6.6908)	0.3124 (2.6814)
Greatest skull length	0.7440 (0.6660)	0.3350 (0.2998)
C ₁ M ₃ length	−0.5234 (−0.8375)	0.1362 (0.2180)
Mesopterygoid fossa breadth	0.3390 (1.1297)	0.3364 (1.1209)
Constant	−23.8467	−50.7967
Variance explained (%)	60.7	33.0

unidentified MZB Timor group; *P. l. lombocensis*; *P. l. heudei*; *P. t. temmincki*; *P. griseus griseus*; and *P. g. pallidus*) and five selected characters (rostrum length; P³ breadth; greatest skull length; C₁M₃ length; and mesopterygoid fossa breadth). This DFA extracted four significant functions, which combined explained 99.9% of the variation. The separation between these six taxon/groups was clearly apparent from the plot of Function 1 and 2 (Figure 2). The unidentified Timor group clearly clustered close to *P. l. lombocensis* and *P. l. heudei* and was a form of *P. lombocensis*. Function 1, which explained 60.7% of the variance, clearly separated the *P. lombocensis* from both *P. temmincki* and *P. griseus*. The characters loading most heavily (>0.5) were P³ breadth, greatest skull length, rostrum length and C₁M₃ length (Table 1). Function 2, which explained 33.0% of the variance, clearly separated *P. temmincki* and *P. griseus*. The character loading most heavily (>0.5) on Function 2 was rostrum length (Table 1). A total of 93.6% of individuals were classified to their correct group/taxon. Two of 20 *P. l. heudei* misclassified to the Timor form of *P. lombocensis* and two of the 10 *P. g. griseus* misclassified to *P. g. pallidus*.

The *Pteropus lombocensis* Group

The sample of one male and nine female *P. lombocensis* specimens from Timor preclude an analysis of sexual dimorphism in this sample. However, males and females were combined in this sample following the absence of observed sexual dimorphism in *P. l. lombocensis* and *P. l. heudei* by Kitchener *et al.* (1995a).

A DFA based on the three forms of *P. lombocensis* (the Timor form, *P. l. lombocensis* and *P. l. heudei* – including Komodo) and five selected skull and dentary measurements (C₁M₃ length; M¹ length; mesopterygoid fossa breadth; braincase breadth; and rostrum length) extracted two very significant Functions. Function 1, which explained 84.9% of

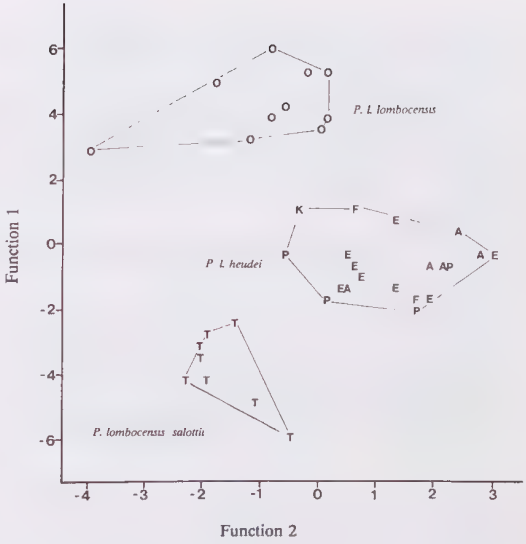


Figure 3 Plot of Functions 1 and 2 from DFA based on the three *P. lombocensis* subspecies (*P. l. lombocensis*, *P. l. heudei* and *P. l. sallottii*) and five selected skull characters (see text). Island codes as for Figure 2.

the variance, separated each of these forms (Figure 3). The characters loading most heavily (>0.5) on Function 1 were C₁M₃ length and braincase breadth (Table 2). Function 2, which explained 15.1% of the variance, partially separated *P. l. heudei* from the other two forms (Figure 3). The characters loading most heavily (>0.5) on Function 2 were mesopterygoid fossa breadth, M¹ length and C₁M₃ length (Table 2). The DFA allocated all specimens to their correct group.

Summary of the multivariate analysis

The above analyses indicated that the MZB Timor specimens clustered closely in discriminant function space with *Pteropus lombocensis* but were

Table 2 Canonical Variate Function Coefficients from DFA between three groups of *P. lombocensis* [(i) Timor; (ii) Lombok; and (iii) Komodo, Flores, Lembata, Pantar, Alor] and based on five cranial characters (see text). Standardised values followed by (in brackets) unstandardised values.

Character	Function 1	Function 2
C ₁ M ₃ length	1.0847 (3.1533)	−0.6713 (−1.9513)
Braincase breadth	0.7276 (1.6337)	0.2222 (0.4990)
Mesopterygoid fossa breadth	−0.0025 (0.0080)	0.8745 (2.8395)
M ¹ length	0.1323 (0.3851)	0.8612 (2.5064)
Rostrum length	−0.1786 (−0.3192)	0.4564 (0.8157)
Constant	−98.8921	−11.6914
Variation explained (%)	84.9	15.1

phenetically not close to either *P. temmincki* or *P. griseus*. They were phenetically closer to *P. l. heudei*, the eastern subspecies, than to *P. l. lombocensis*. The Komodo specimen was allocated to *P. l. heudei* by DFA. The Banda Neira form of *P. griseus* (*pallidus*) clustered close to the nominate form on Timor, Semau, Roti and Wetar but is recognised by us as a subspecies.

The Timor form of *P. lombocensis* is described below as a new subspecies by D.J. Kitchener.

SYSTEMATICS

Pteropus lombocensis salottii subsp. nov.
Kitchener

Holotype

Museum Zoologicum Bogoriense No. MZB 2195 adult male; skull and dentaries separate; skin prepared as 'cabinet' skin; collected on 3 February 1929 by Mrs Walsh.

Type locality

Soe, W. Timor, Nusa Tenggara Timur, Indonesia (9°51'S, 124°16'E); from an altitude of 880 m.

Paratypes

(All adult females from the type locality and collected on the same date as the holotype). MZB 2182, 2184, 2189–94, 2196.

Diagnosis

Similar in pelage colouration to *Pteropus lombocensis lombocensis* and *P. l. heudei* but differing

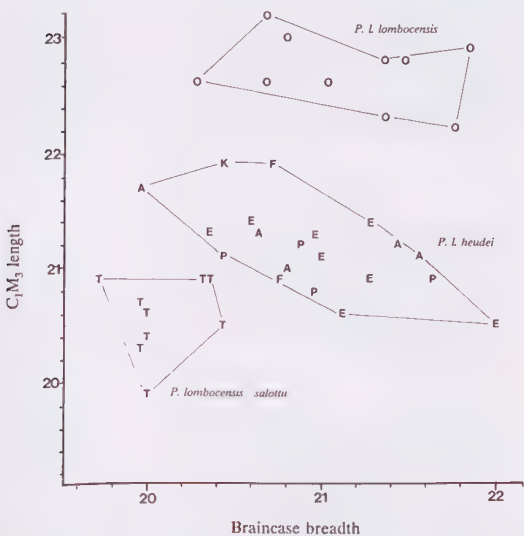


Figure 4 Plot of C₁M₃ length versus braincase breadth for the three subspecies of *Pteropus lombocensis*. Island codes as for Figure 2.

from both these subspecies in averaging smaller in all skull, dentary and dental characters, except P⁴P⁴ width (Table 3) and by having C₁M₃ shorter relative to braincase breadth (Figure 4).

It also differs from *P. l. lombocensis* by being absolutely smaller in condylobasal length, C¹M² length, C₁M₃ length and M¹ length (Table 3).

Distribution

Known only from Soe, West Timor.

Etymology

Named after Mr Mark Salotti in recognition of his work in contributing towards the curation of the mammal collections from Indonesia made between 1987 and 1993.

Remarks

Pteropus lombocensis is readily distinguished from both *P. temmincki* and *P. griseus* on overall body size and pelage colouration and on skull and dental measurements as described in Andersen (1912). Our measurements confirm that *P. lombocensis* differs from *P. temmincki* in having a number of skull and dentary measurements that are different, particularly a larger P³ breadth, coronoid height and greatest skull length and a smaller orbit diameter (see Table 3). It also differs from *P. griseus* in a number of measurements, particularly in having a shorter rostrum length and forearm length (Table 3).

Discussion

Previously *Pteropus lombocensis* was thought to be restricted to the volcanic islands of the inner Banda Arc from Lombok Island in the west to Alor Island in the east (Kitchener *et al.* 1995a). Its discovery on Timor Island in the Gondwanic outer Banda Arc, where it has differentiated morphologically into a distinct subspecies, follows a pattern that is commonly repeated for bats in this region. There is a trend for Nusa Tenggara bats to so differentiate in the eastern parts of the inner Banda Arc and between the inner and outer Banda Arcs (e.g., Kitchener *et al.* 1995a,b,c; Kitchener and Maharadatunkamsi (in prep.).

Goodwin (1979) recorded the distribution of *P. g. griseus* as Timor, Semau, Bonerate, Djampea and possibly Saleyer islands. Its occurrence also on Roti and Wetar Islands suggests that it will probably also be found on other islands in the inner Banda Arc.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of Mr A. Reeves, Director, Western Australian Museum; Drs M. Amir, Director, Balitbang Zoologi (LIPI); and

the then Directors of the Department responsible for the conservation of wildlife in Nusa Tenggara Barat, Ir P. Supriadi and Nusa Tenggara Timor, Ir J. Mochtar. To our colleagues Dr R. How and Mr R. Johnstone, Western Australian Museum; Mr A. Gunnell, Curtin University of Technology and Drs A. Suyanto, Ir Maharadatunkamsi, and Bapak Boeadi, Museum Zoologicum Bogoriense, who participated in the field work, we extend our thanks for both their effort and companionship.

We thank Dr Soetikno, Kepala, Puslitbang Biologi, LIPI, for the loan of the MZB specimens.

Expedition costs were defrayed by grants to the senior author from: National Geographic Society, Washington, Australian National Parks and Wildlife Service and the Scott Trust, Sydney. Garuda Indonesia kindly defrayed freight costs of the expeditions. Additional skulls were prepared by Mr M. Salotti, Western Australian Museum. All measurements were recorded by Dr W.C. Packer, Western Australian Museum. Mrs N. Cooper assisted with statistical analyses. Mrs A. Nevin, Western Australian Museum kindly typed the manuscript.

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Manuscript received 27 September 1994; accepted 28 October 1994.

New species and records of cockroaches from Western Australia (Blattaria)

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Abstract – Three new species of cockroaches from Western Australia are described, namely *Hensausseura humphreysi* (Blattellidae) and two cavernicolous taxa, *Nocticola brooksi* (Nocticolidae) and *Neotemnapteryx wynnei* (Blattellidae). A few new records of some Western Australian Blattidae: Polyzosteriinae, and Blattellidae are given.

INTRODUCTION

This paper presents the results of a study of some cockroaches that were sent to me for identification by Dr W.F. Humphreys of the Western Australian Museum. It was expanded to include a few specimens from other museums but I have generally restricted the work to species found in Western Australia.

Specimens were borrowed from the following museums through the courtesy of their curators or collection managers: ANIC = Australian National Insect Collection, Canberra, ACT, Australia; Dr David Rentz. MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. NMV = Museum of Victoria, Melbourne, Victoria, Australia; Ms Catriona McPhee. NTM = Northern Territory Museum, Darwin. PMYU = Peabody Museum of Natural History, Yale University, New Haven, CT, U.S.A.; Dr Charles Remington. WAM = Western Australian Museum, Perth, Western Australia; Dr W.F. Humphreys.

SYSTEMATICS

Family Nocticolidae Bruner

Genus *Nocticola* Bolívar

Nocticola Bolívar: Roth, 1988: 298 (diagnosis).

Remarks

There are three described Australian species of *Nocticola* of which two, namely *australiensis* Roth (cavernicolous) and *babindaensis* Roth (epigean) are from Queensland (Roth 1988: 302, 303), and *flabella* Roth (cavernicolous) is from Western Australia (Roth 1991a: 17). Two additional species have been found in Western Australia, one of which is described and named below.

Nocticola brooksi sp. nov.

Figures 1A–E

Material Examined

All specimens were collected in caves in the northern Kimberley of Western Australia and in the Northern Territory near Katherine. The material is preserved in alcohol, except for a male, female, and nymph that were cleared and mounted on slides in Permout. Figures 1A–E were drawn from slide mounted specimens.

Holotype

♂ (in alcohol), Cave KNI-41, Western Australia, Australia, 15°11'S, 128°38'E, 20 June 1994, R.D. Brooks, BES 3191 (WAM 94/1945).

Paratypes

Australia: Western Australia: The following specimens (nymphs and adults) have a small dark eye spot behind the antenna: KNI-19, 15°18'S, 128°37'E (BES: 2743, 2765, 2829, 2884, 3042, 3046, 3129, 3169, 3174, 3182, 3269): 1 nymph, 7 May 1994; 5 nymphs, 8 May 1994; 2 nymphs, 10 May 1994; 1 ♀, 16 May 94; 2 ♂♂, 1 ♀, 12 nymphs, 12 June 1994; 1 nymph, 6 June 1994; 2 ♀♀ (one on slide 28), 8 nymphs, 19 June 1994, R.D. Brooks; 1 ♂, 3 nymphs, 6 June 1994, W.F. Humphreys, R.D. Brooks, B. Vine; 1 ♂ (on slides 26a, 26b), 1 ♀ nymph (on slide 27), 19 June 1994, Wendy Binks; 3 nymphs, 19 June 1994, B. Jones; 1 nymph, 29 June 1994, W. Binks. KNI-19, 15°18'S, 128°37'E (BES: 2820, 2866): 1 nymph, 10 May 1994, B. Vine; 1 nymph, 15 May 1994, W.F. Humphreys. KNI-27, 15°17'S, 128°41'E (BES: 2876, 3022, 3028): 1 nymph, 16 May 1994; 3 nymphs, 6 June 1994, R.D. Brooks; 1 nymph, 6 June 1994, Trish Handasyde. KNI-41, 15°11'S, 128°38'E (BES: 3061, 3069, 3071, 3084, 3086, 3088, 3186, 3191, 3282): 1 ♀, 5 nymphs, 20 June 1994, W. Binks; 1

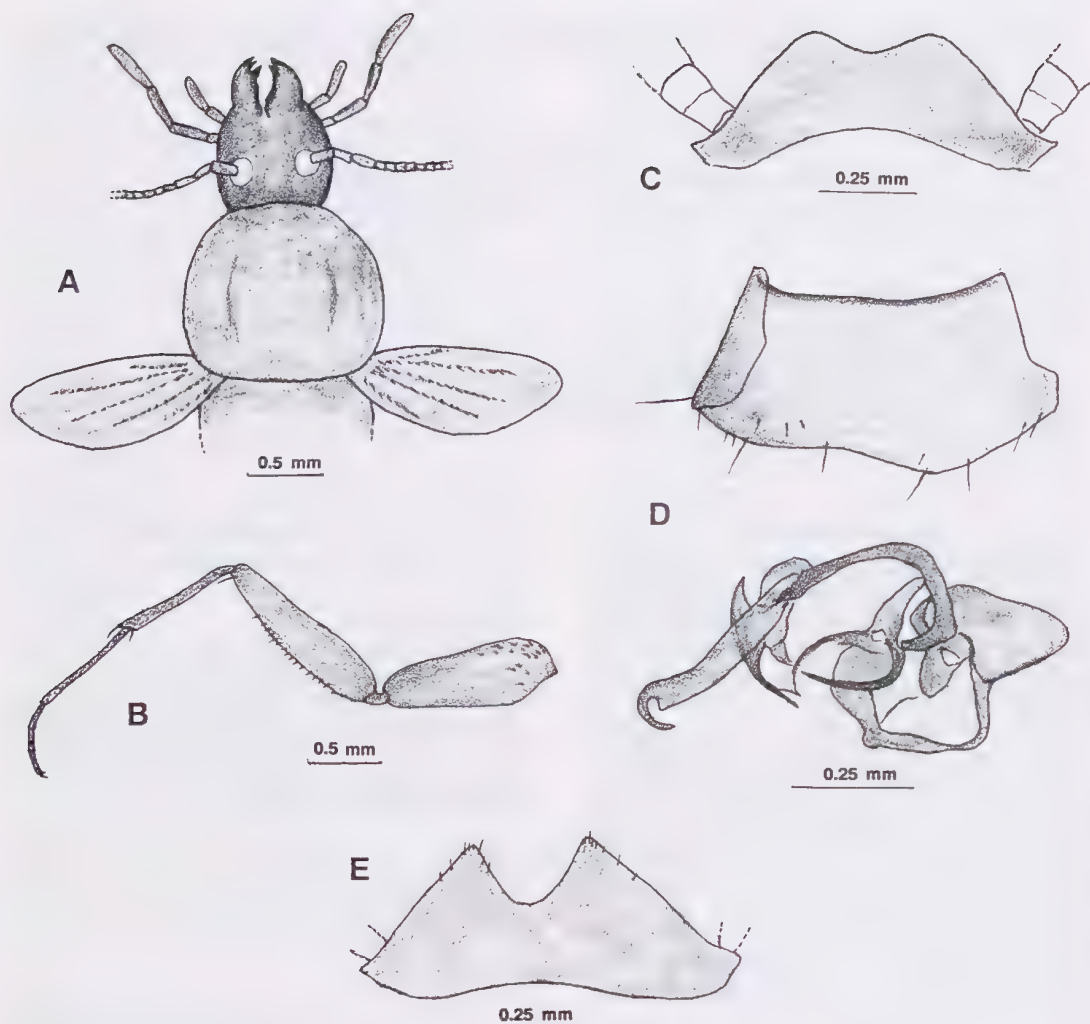


Figure 1 *Nocticola brooksi* sp. nov., paratypes from north Kimberley caves. A–D, male: A, head, pronotum, and tegmina (dorsal; the head is extended forward); B, front leg (anterior surface); C, supraanal plate (dorsal); D, subgenital plate (top) and genitalia (bottom) (dorsal); E, female, supraanal plate (dorsal).

nymph, 20 June 1994, R.D. Brooks; 1 ♀, 10 nymphs, 29 June 1994, W. Binks; 3 nymphs, 7 June 1994; 1 nymph, 8 June 1994, W.F. Humphreys; 1 nymph, 7 June 1994; 1 nymph, 8 June 1994, B. Vine; 4 nymphs, 7 June 1994; 5 nymphs, 8 June 1994, R.D. Brooks. The Tunnel (in the Oscar Range in the Western Kimberley, about 600 km to the southwest of Ningbing), KO-1 (BES 3341): 2 nymphs, 8 July 1994, R.D. Brooks. LCB1, 15°11'S, 128°37'E (BES 3095): 2 nymphs, 8 June 1994, R.D. Brooks. All lodged in WAM.

Northern Territory: The following specimens lack minute eye spots and were collected in Cutta Cutta Cave, 14°35'S, 132°25'E (near Katherine about 600 km east of Ningbing), 8K-1 (BES: 3203, 3219,

3227, 3234, 3244, 3287): 5 nymphs, 25 June 1994; 2 nymphs, 26 June 1994, R.D. Brooks; 5 nymphs, 25 June 1994; 8 nymphs, 26 June 1994, W. Binks; 3 ♀, 4 nymphs, 25 June 1994, B. Vine; 1 nymph, 25 June 1994, B. Jones. All lodged in WAM and NTM.

Diagnosis

Cavernicolous. Male: Eyes represented by a few minute black ommatidia (however, see female, below). Tegmina reduced, reaching to about the first abdominal tergum, membranous, with veins reduced, setose, hind wings absent. Front femur Type C_1 , pulvilli and arolia absent, tarsal claws simple, symmetrical, minute. Abdominal terga unspecialized. Styli absent. Female: Eyes as in male,

except in Cutta Cutta Cave specimens which completely lack ommatidia. Apterous. Hind margin of supraanal plate distinctly, concavely excavated.

Description

Male

Head exposed, eyes represented by a few minute, black ommatidia located behind the antennal socket (these black dots disappear when the specimen is treated with KOH and cleared in slide preparation). Pronotum suboval (Figure 1A). Tegmina greatly reduced reaching only to about the first abdominal tergum, membranous, 5 setose veins present (Figure 1A). Hind wings absent. Legs with femora not uniformly slender, tapering distad, anteroventral margin of front femur with a row of minute piliform spinules terminating in a stout spine (Type C₁), pulvilli and arolia absent, tarsal claws minute, simple, symmetrical (Figure 1B). Abdominal terga unspecialized. Supraanal plate transverse, hind margin shallowly, concavely excavated (Figure 1C). Subgenital plate with hind margin weakly uneven, styli absent (Figure 1D, top). Genitalia as in Figure 1D, bottom; genital hook on the left side. Colouration, yellowish.

Female

Eyes with a few dark ommatidia as in males, these completely absent from Cutta Cutta Cave females. Apterous. Hind margin of supraanal plate deeply concavely excavated (Figure 1E).

Nymphs

The immatures are white. All stages including what are probably first instars have the minute black ommatidia, but these are lacking from Cutta Cutta Cave specimens. The hind margin of the supraanal plates of both sexes are not distinctly excavated and appear to be convexly rounded.

Measurements (mm) (♀ in parentheses)

Length, 4.3 (4.8–5.7); pronotum length x width, 1.3 x 1.5–1.6 (1.4–1.7 x 1.7–2.0); tegmen length, 1.1–1.5.

Etymology

The species is dedicated to Mr R. Darren Brooks who collected the holotype.

Remarks

The absence of a male tergal gland places *brooksi* in the *simoni*-species-group (Roth 1988). This new species keys to couplet 2 in the key to male Australian *Nocticola* (Roth 1991a: 21), where it can be separated from *N. flabella* by differences in the shape and texture of the reduced tegmina and

shape of the supraanal plate. The females can be separated by differences in the shapes of the supraanal plates.

It is interesting that nymphs and adult females (males were not collected) from Cutta Cutta Cave all lack the few minute ommatidia that are found in adult males, females, and nymphs from all other localities. The reason for this complete loss of eyes in the Cutta Cutta Cave is unknown. Humphreys (personal communication) speculates that "eye" retention in *Nocticola* may be connected with the openness of the cave system where light is intermittent. The Cutta Cutta Cave is totally dark.

The following information regarding the three distinct cave areas in which *brooksi* was collected was kindly supplied by Dr W.F. Humphreys:

Cutta Cutta Cave (8K-1) is a fully developed cave system with some depth. It is totally dark, except where it is lit as a tourist cave, and connects to permanent water in a joint controlled phreatic system.

Caves in the Ningbing Ranges (prefix KNI-) are part of a Devonian reef complex.

For the most part they are grike developments which are frequently open to the surface so that there is intermittent light. Although this is not the case in some caves (e.g., KNI-19 and KNI-41), these populations are probably in continuity with those inhabiting the more open systems. The specimens were collected in the dry season so that the more open systems had become too dry to retain their populations – only the deeper recesses of the grike developments and the proper caves were still moist enough to have cavernicolous populations.

The Tunnel (KO-1) is in the Oscar Range which is part of a Devonian reef system that is separated by 550 km from a similar system in the Ningbing Ranges. It is a minor stream that cuts through the reef in a massive tunnel, but a minor side passage was humid.

Nocticola sp.

Material Examined

Australia: Western Australia: Barrow Island: Cave B-1, 20°48'S, 115°19'E: 1 nymph, 10 September 1991, BES: 297 (WAM 92/55); 1 ?♀, 12 September 1991, W.F. Humphreys, B. Vine, BES: 313 (WAM 92/56); 2 nymphs, Lower (mud) chambers, 17 September 1991, D. Goodgame, BES: 326 (WAM 92/57-8); Cape Range Peninsula: 1♀, Cave C-15, 22°13'S, 113°59'E, 29 May 1990, CR 1990: 218 (WAM); 1♀, Cave C-64, 22°03'S, 114°01'E, 25 May 1990, D. Brooks, CR 1990: 217 (WAM). All specimens in alcohol.

Remarks

All specimens are small (length about 4 mm or

less), white, eyeless, and lack tegmina and wings; in one specimen the posterior corners of the mesonotum are produced and appear to be nymphal tegminal pads which suggests that it is an immature male. Adult males of *Nocticola* may have fully developed tegmina and wings or their tegmina may be variably reduced and wings variably reduced or completely absent. Adult females are apterous. It is likely that the above specimens represent an undescribed species but adult males are needed to adequately describe a species in this genus.

Family Blattellidae

Subfamily Blattellinae

Genus *Hensaussurea* Princis

Hensaussurea Princis: Roth, 1991b: 625 (revision).

Remarks

There are 11 previously described species of *Hensaussurea*, all found in the southern half of Australia (Roth 1991b, fig. 45). Four species occur in Western Australia and of these at least three occur in the southwestern corner of the state. The new species, *humphreysi* described below also occurs in the southwestern part of Western Australia.

Hensaussurea humphreysi sp. nov.

Figures 2A–D

Material Examined

Holotype

♂, Perth, Kings Park, Western Australia, Australia, flight intercept-trough trap, ANIC 1047, January–February 1985, G.P. Hall (ANIC).

Paratypes

Australia: Western Australia: 3♂♂, same data as holotype, 3♂♂ (1 with terminalia slide 351), 1♀, 5 nymphs (1♂ each in WAM and MCZ, remainder in ANIC).

All specimens were originally preserved in alcohol and then pinned; colour may have been altered by the fluid.

Description

Male

Head hidden under pronotum (Figure 2B). Interocular space about the same as distance between antennal sockets (Figure 2A). Pronotum subparabolic (Figure 2B). Tegmina reduced to lateral pads, completely separated from the mesonotum, and reaching to or slightly beyond

hind margin of the mesonotum. Hind wings absent (Figure 2B). Front femur Type B2, with four large proximal spines; pulvilli present on four proximal tarsomeres; tarsal claws symmetrical, simple, arolia present. Abdominal terga unspecialized. Supraanal plate trigonal, apex with a shallow U-shaped excavation forming two small lobes, and a few short setae on either side of the excavation; paraprocts dissimilar, both with spinelike processes (Figures 2B, C). Subgenital plate with strongly dissimilar styli, the right one elongated with a few large spines along the margins, the spinelike apex directed towards the left and reaching the much smaller, cylindrical left style (Figure 2D). Genitalia as in Figure 2D: hook on the left side, with a preapical incision; median phallomere distally enlarged, tapering to an acute apex; right phallomere with two principal sclerites one of them a large cleft structure; overlying the right phallomere is a membrane bearing four spines. Colour pale with dark markings: Head with pale occiput, a dark brown longitudinal band extending from the vertex to the lighter clypeus, labrum lighter brown, cheeks white (Figure 2A). Pronotal disk with a light brown macula on distal half, surrounded by a dark brown band, lateral and anterior borders white; the lateral pale borders of the pronotum continue on the tegmina and metanotum, and more narrowly on the abdominal terga; the mesonotum has two and metanotum four brown dots. The lateral pale margins of the abdominal terga are succeeded mesad by a dark brown longitudinal band, then by a large light brown middle zone (Figure 2B). Abdominal sterna brown, lateral margins pale. Cerci dorsally with two black basal segments, the remainder white, ventrally the cercomeres are dark brown on basal halves, and pale distally. Legs pale, without markings.

Female

Supraanal plate with apex shallowly excavated. Abdominal terga dark brown except for pale lateral borders, and a pale macula on either side of the midline on segments 1 and 2; supraanal plate with a white macula on distomedial region.

Nymph

The nymph resembles the adult (the colour pattern may differ only slightly) except for the complete absence of tegmina.

Measurements (mm) (♀ in parentheses)

Length, 6.0–6.3 (ca. 6.0); pronotum length x width, 1.8–2.1 x 2.6–2.9 (2.1 x 3.0); tegmen length x width, 1.0–1.4 x 0.4–0.7 (1.0 x 0.6); interocular width, 0.6–0.7 (0.7).

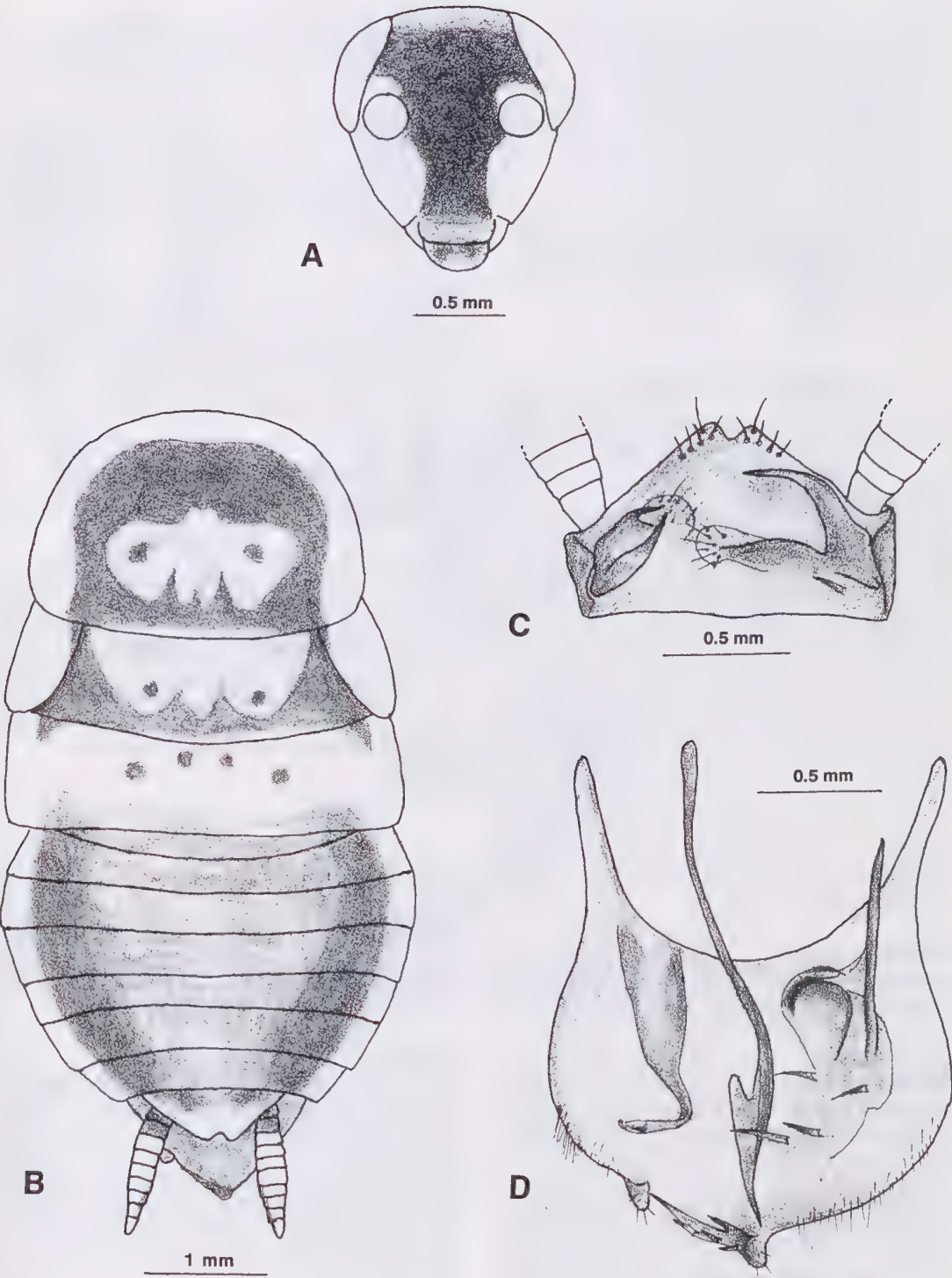


Figure 2 *Hensaussurea humphreysi* sp. nov. A, B, ♂ holotype, head and habitus respectively; C, D, ♂ paratype: C, supraanal plate and paraprocts (ventral); D, subgenital plate and genitalia (dorsal).

Remarks

The strongly dissimilar male styli places *H. humphreysi* in the *tricolor*-species-group. The species keys out to couplet 4 (Roth 1991b: 626) where it can be separated from *H. halmaturina* Shelford (*halmaturina*-species-group) by the dissimilar styli, and colour pattern differences.

Etymology

The species is dedicated to Dr W.F. Humphreys, senior curator at the Western Australian Museum, who has sent me many cockroach specimens from Western Australia.

Hensaussurea pedestris Princis

Hensaussurea pedestris Princis: Roth, 1991b: 630, figs. 47F, 48 (redescription: male and female).

Material Examined

Australia: Western Australia: Cape Range Peninsula: 1♂, camp, at night, 22°01'S, 114°03'E, 20 May 1990, J.M. Waldock, C.R. 90 #158 (WAM); 5 nymphs, Site TL-3, 22°15'S, 114°04'E, 17 May-5 June 1990, J.M. Waldock (WAM); 1♀, Site TL-4, 22°06'S, 114°00'E, pitfall traps, 17 May-3 June 1990, J.M. Waldock (WAM); 1♀, Site TL-5, 22°06'S, 114°00'E, litter, 3 June 1992, J.M. Waldock (WAM); 1♂, 1 nymph, Site TL-7, pitfall traps, 22°15'S, 114°04'E, pitfall traps, 20 May-5 June 1990, J.M. Waldock (WAM).

Hensaussurea peniculus Roth

Hensaussurea peniculus Roth, 1991b, 631, fig. 49 (male and female).

Material Examined

Australia: Western Australia: 1♀, Cape Range Peninsula, Site TL-4, pitfall traps, 22°06'S, 114°00'E, 17 May-3 June 1990, J.M. Waldock (WAM).

Measurements (mm)

Length, 7.0; pronotum length x width, 2.0 x 2.6 (sides deflexed); tegmen length x width, 1.3 x 0.9.

Remarks

The colour of this female differs somewhat from the unique female paratype. The pro- and mesonotum are yellowish and have a narrow dark brown transverse band on their hind margins. The first six abdominal terga are infuscated laterally, and segments seven to ten are yellowish and yellowish-white. Cerci are yellow on both surfaces. The specimen is slightly smaller than the paratype.

Paratemnopteryx sp. 1

Paratemnopteryx sp. 1 Roth, 1990: 580, figs 26A-C (male and female).

Material Examined

Australia: Western Australia: 1♀, Eneabba region, Cave E-22, 1 June 1991, C. Rippon (WAM); 1♂, Cape Range Peninsula, Cave C-79, 22°06'S, 14°00'E, 27 June 1989, W.F. Humphreys, R. Wood, CR'89 #3205 (WAM).

Remarks

This unnamed species combines characters of *P. australis* Saussure and *P. rufa* (Tepper). It was previously reported from Queensland (pitfall traps) and Northern Territory (bat caves). Its eyes are fairly well developed.

Genus *Neotemnopteryx* Princis

Neotemnopteryx Princis: Roth, 1990: 535 (revision).

Remarks

There are ten previously known species of *Neotemnopteryx*, most of them occurring on the eastern coast of Australia; one of them, *N. douglasi* (Princis), is cavernicolous, and with another species, *N. fulva* (Saussure), occur on the southwestern coast of Western Australia (Roth 1990, fig. 34). The following new species is the second cave dwelling member of the genus.

Neotemnopteryx wynnei sp. nov.

Figures 3A-F

Material Examined

Holotype

♂, Cave 6N-747, eastern extension, 70 m from entrance, Nullarbor Plain, Western Australia, Australia, 2 January 1994, R. Wynne (S47), BES: 1256 (WAM 94/714).

Diagnosis

Cavernicolous. Male: Eyes absent. Tegmina reduced, widely separated, hind wings vestigial. Front femur Type A₃, pulvilli and arolia absent. Supraanal plate hind margin convexly rounded, entire. Subgenital plate trigonal; styli dissimilar, the right one slightly larger and at the apex of the plate, apices with numerous small black spines. Reddish brown.

Description

Male

Head exposed; eyes absent (Figure 3B); antennae filamentous. Pronotum subparabolic (Figure 3A).

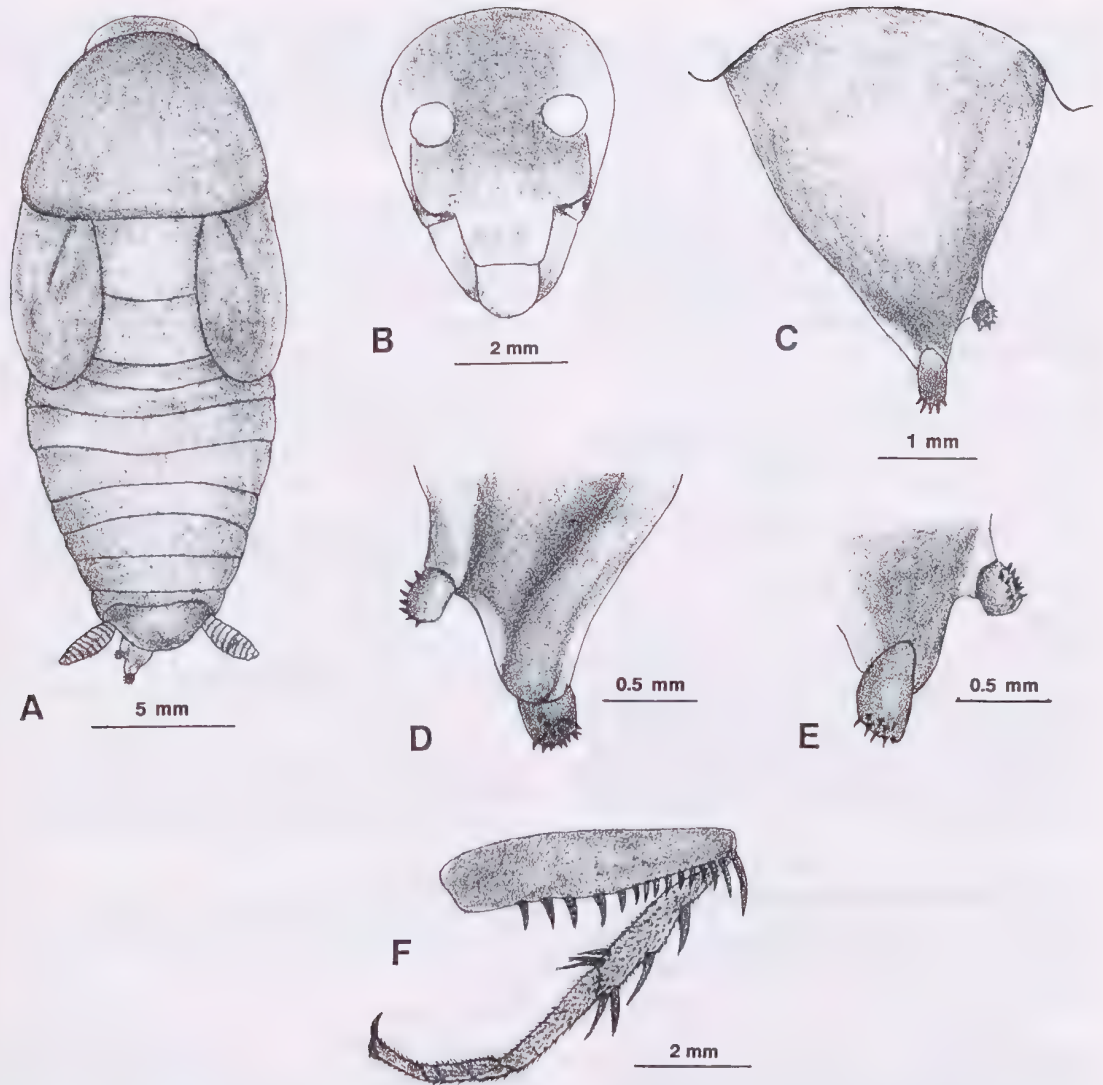


Figure 3 *Neotemnopteryx wyynnei* sp. nov., ♂ holotype: A, habitus; B, head; C, subgenital plate (ventral); D, E, apex of subgenital plate showing styli (dorsal and ventral respectively); F, front leg (anterior view; coxa and trochanter not shown).

Tegmina reduced to well separated lateral, coriaceous pads, apices rounded, reaching to middle of second abdominal tergum (Figure 3A). Hind wings vestigial, narrow, hidden under tegmina, reaching to hind margin of first abdominal tergum. Front femur Type A3, five proximal spines widely spaced, succeeding row of seven smaller, equally long spines closer together; pulvilli and arolia absent, tarsal claws simple, symmetrical (Figure 3F); basitarsus of front leg about equal in length to the others combined (Figure 3F), of the mid and hind legs slightly longer than the others. Abdominal terga unspecialized (Figure 3A). Supraanal plate with hind margin

convexly rounded, entire, not reaching apex of protruding subgenital plate (Figure 3A). Subgenital plate convex, trigonal, the sides at the apex thickened into rounded ridges; styli dissimilar, small, bulbous, sclerotised, both with numerous small dark spines, the right style larger at the apex of the plate, the smaller one a short distance to its left (Figures 3C–E). Colouration: Dark reddish brown. Head reddish brown with “ocular” area and clypeus, labrum, and mandibles lighter, yellowish (Figure 3B).

Female
Unknown.

Measurements (mm)

Length, 23.2; pronotum length x width, 6.8 x 8.8; tegmen length x width, 7.3 x 3.4; hind wings vestigial, hidden under tegmina.

Remarks

The other cavernicolous species in *Neotemnopteryx*, namely *douglasi* (Princis) (= *Shawella douglasi* Princis), from Jurien Bay, Western Australia, is distinctly different from *N. wyneii*, and has reduced eyes, longer tegmina, and a large densely setose tergal gland on the first segment (Roth 1990: 556).

Etymology

The species is dedicated to its collector, Mr Richard Wynne, a young speleologist.

Genus *Trogloblattella* Mackerras

Trogloblattella Mackerras, 1967a: 39.

Remarks

There is only one species in this monotypic genus, namely *T. nullarborensis* Mackerras, and it is found only in Western and South Australia. *Trogloblattella chapmani* Roth was described from limestone caves in Sarawak (Roth 1980: 97) but this species has been transferred to *Neotrogloblattella* Roth (Roth 1991c: 1017).

Trogloblattella nullarborensis Mackerras

Trogloblattella nullarborensis Mackerras, 1967a: 39, pl. 1A–D, figs 1–6; Roth, 1990: 558, Figures 15A–I, 35

Material Examined

Australia: Western Australia: Nullarbor Plain: 1♀, 1♀ nymph, Cave 6N–707, terminating chamber, 700 m from 10 m vertical entrance, ca. 30 km N. of Mundrabilla Homestead, 28 December 1993, BES.1254, (L13) (WAM); 1♂, same data except BES.1255 (M11), Norm Poulter (WAM); 1♀ nymph, Cave 6N–36, dark zone, ca. 10 m from entrance, 4 January 1994, M. Melh, BES.1258 (WAM); 1♀, Cave 6N–37, between the drop off and camp, 5 January 1994, BES.1259 (L2), N. Poulter (WAM); 1 nymph, Cave 6N–748, dark zone ca. 30 m from entrance, 3 February 1994 (S76), R. Wynne (WAM).

Subfamily Pseudophyllodromiinae

Ellipsidion humerale (Tepper)

Ellipsidion humerale (Tepper): Hebard, 1943: 110, Pl. XII, fig. 10; Princis, 1969: 986 (literature).

Material Examined

Australia: Western Australia: Cape Range Peninsula: 1♀ (tegmina and wing on slide 25), camp, near 22°15'S, 114°03'E, headtorch, 21 May 1990, Brooks, CR 90 #135 (WAM).

Remarks

The species has also been recorded from Northern Territory, and Central and Western Australia. The type specimen is a female from "Northern Territory of South Australia". Hebard suggested that *E. laetum* Hanitsch, from Burnside, Northern Territory may be a variant of *humerale*.

There is considerable colour variation in this species and Hebard suggested that those from Western Australia may represent a more western race or species but that a "Detailed consideration of large series is necessary to determine which." I have available a large number of specimens from different localities and time permitting hope to study the variation in colour, size, and genitalia in this taxon.

Family Blattidae

Subfamily Polyzosteriinae

Drymaplaneta semivittata (Walker)

Drymaplaneta semivittata (Walker): Mackerras, 1968b: 547, figs 37a–c, 45, 91 (male and female).

Material Examined

Australia: Western Australia: 1♀, Triggs, near Perth, 5 December 1965, Ch. Morris (PMYU).

Remarks

This species is confined to the south-western part of Western Australia, where apparently it is a common domestic pest throughout Perth and other settlements.

Platyzosteria (Melanozosteria) ?*nigrofasciata* (Shaw)

Platyzosteria (Melanozosteria) *nigrofasciata* (Shaw): Mackerras, 1968a: 285, figs 87, 102, 120, pl. 2G (redescription: male and female).

Material Examined

Australia: Western Australia: 1♂, Cape Range Peninsula, near Cave C–60, 22°06'S, 113°59'E, 17 May 1990, J. Waldock (WAM).

Remarks

This specimen keyed closest to *nigrofasciata* (Mackerras 1968a: 240). However, the hind margin of its vestigial tegmina are separated from the

mesonotum by a little more than half its length (rather than about one third; see fig. 120 in Mackerras, 1968a) and the middle of the pronotal disk is yellowish rather than solidly dark (pl. 2G in Mackerras 1968a).

***Platyzosteria (Leptozosteria) spenceri* Shelford**

Platyzosteria (Leptozosteria) spenceri Shelford: Mackerras, 1967b: 1295, figs 104, 110, pl. 4, figs 4, 5 (redescription).

Material Examined

Holotype

♂ (probably a nymph), "Central Australia", Spencer Gillen Expedition, 1901–02 (NMV).

Other Material

Australia: Northern Territory: 1 nymph, base of Ayers Rock, 22 May 1954, C.A., Geelong College Expedition (NMV). **Western Australia:** 1 ♀ nymph, nr. Boonbooa Pool, Pigandy Creek, Ashburton District, 27 August 1975, P.C. and C.W. Kendrick (WAM 92/659); 1 nymph, 130 miles SE. of Broome, September, A.S. Cudmore (NMV).

Remarks

The species is known only from nymphs and has been reported from Northern Territory, South Australia, and Western Australia.

***Zonioploca pallida* Shelford**

Zonioploca pallida Shelford: Mackerras, 1965: 911, figs 5, 14, 23, pl. 1, figs 5, 6 (redescription, male and female).

Material Examined

Australia: Western Australia: 1 ♀ (with ootheca), Perth, 15 October 1931, Darlington, Australia/Harvard Expedition (MCZ).

Remarks

The species is restricted to the southwestern corner of Western Australia.

ACKNOWLEDGEMENTS

I thank Dr W.F. Humphreys and others who sent me specimens. I am grateful to the Australian Biological Resources Study (ABRS) for partial financial support.

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A new *Catasarcus* species (Coleoptera: Curculionidae: Entiminae) from the Shark Bay – Kalbarri region of Western Australia

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Abstract – *Catasarcus militaris*, a new species of apterous weevil from near mid-west coastal Western Australia, is described and the holotype and male genitalia are figured. A distribution map is included for it and four similar allopatric *Catasarcus* species, including three informally designated the *C. marginispinis* species-group. Diagnoses are provided for six taxa, including a less closely allied species that is the only *Catasarcus* known to be sympatric with *C. militaris*. Brief ecological notes on *C. militaris* are provided.

INTRODUCTION

The Australian endemic, apterous weevil genus *Catasarcus* Schoenherr was most recently revised by Thompson (1968) who considered it to contain 42 valid taxa, of which all but four are confined to Western Australia. No further species have been described since that time and many remain poorly known, despite considerable additional collecting in previously unsampled areas. During a field trip to the Shark Bay region in early December 1988 I collected a small number of *Catasarcus* specimens, several of which proved, upon closer examination, to belong to an undescribed “quadrispinate” species. An additional 10 specimens of this new taxon, from another (more southern) locality, were later found in the Western Australian Museum collection. These 13 specimens form the basis for the following description.

MATERIAL AND METHODS

Specimen measurements are linear and have been measured to the nearest 0.05 mm with an eyepiece graticule on a Zeiss stereomicroscope. For comparative purposes, description format and morphological terminology/measurements conform to Thompson (1968), with text abbreviations (capitalised in parentheses) and further definitions of character measurements as follows: total length (TL) – from anterior margin of epistome to elytral apex in dorsal view; total width (TW) – at widest point of body (elytra) excluding posthumeral spines; elytral length (AC) – see Thompson (1968: 367); anterior spine index (ASI) – see Thompson (1968: 368); posterior spine index (PSI) – calculated by same method as Thompson (1968) used to derive ASI; anterior and posterior dorsal elytral spine lengths (LAS, LPS respectively) – from centre of base (base defined as point where elytral

dorsum abruptly changes angle – i.e. nearest stria puncture) to apex, when viewed dorsally with spine in horizontal plane; distance between posterior dorsal elytral spine bases (IPSB) – from centre of spine base to same; on each elytron, distance between anterior and posterior dorsal elytral spine bases (IAPSB) – as for IPSB; distance between posterior dorsal elytral spine apices (IPSA). The following collection codens are used in the text: CALM – Department of Conservation and Land Management, Woodvale, W.A.; MPWA – author’s collection; WAM – Western Australian Museum, Perth.

SYSTEMATICS

Catasarcus militaris sp. nov.

Figures 1–3

Material Examined

Holotype

♀, 32.3 km NE. of Tamala HS, Western Australia, Australia in 26°32'S, 113°59'E, 10 December 1988, M. Peterson, on leaves of *Grevillea candelabroides* (WAM 90/19).

Paratypes

Australia: Western Australia: 1 ♀ (MPWA) and 1 ♂ (WAM 90/20), same data as for holotype; 2 ♀ and 2 ♂ (WAM 78/40–41, 90/26–27), Carrollgouda Well, Kalbarri area, 30 November 1968, Hale School; 6 ♂ (WAM 78/39, 90/21–25), same data except 28 November 1968.

Diagnosis

A member of the quadrispinate section of *Catasarcus*, though occasional specimens bispinate

(possibly unique in genus) when anterior dorsal elytral spines absent; dorsally with a pronounced, dense scale pattern of pearl-white, pink-brown and blue patches and alternating pearl-white and black-bronze vittae; ovipositor with a flattened blade-like apex. Most like *C. albisparsus* Pascoe, *C. cicatricosus* Pascoe and *C. marginispinis* Pascoe but differs from these by lacking small forwardly directed tubercles at elytral base and possessing pink-brown and blue scales and smaller anterior dorsal spines (<56% of LPS vs >59% of same) set more caudad on elytra (ASI: 50–58 vs 44–54).

Description

TL: 8.8 – 12.1 mm. Body, including lateral post-humeral spines, black; antennae, legs and dorsal elytral spines red to dark red. Scales dense throughout, dorsally forming a constant pattern of alternating black-bronze and brilliant pearl-white vittae and pearl-white, pink-brown and blue patches on a black background (Figure 1); no powdery exudate present. Setae hair-like, conspicuous. Head with frons flat, without a median cariniform elevation; admedian and lateral frontal carinae present, both pairs short, sometimes

obscured by scales, strongly converging anteriorly; frons with numerous conspicuous setae; eyes convex, about 1.3 X as long as broad. Rostrum 1–1.2 X as long as broad, scarcely widening apically; median carina evenly and moderately raised for most of its length, slightly higher than frons and usually more or less parallel with latter in profile view (not arched); chin weak. Mentum with four setae. Antennae with length of funicle segments 1–3 in ratio 2.8 : 1.5 : 1 (mean, $n=13$). Prothorax weakly transverse (length to width ratio, 10 : 14.3–16.8), a little wider at base than apex; post-ocular lobes well developed, angulate. Scutellum smooth, covered in a few ovate scales. Elytra globose-acuminate (length to width ratio, 10 : 6.9–7.4), dorsally quadrispinate or occasionally bispinate when anterior dorsal elytral spines absent; LAS 0–55.6% (mean 29.5%, $n=13$) of LPS, with δ values slightly less than ϕ (0–40% vs 19.4–55.6%); ASI: 50–56 in δ (mean 53.8, $n=8$), 52–58 in ϕ (mean 55.3, $n=4$); LPS 17.1–35.8% (mean 26.1%, $n=13$) of AC, with little overlap between the values of the sexes (δ , 24.4–35.8% vs ϕ , 17.1–25.3%); PSI: 52–58 in δ (mean 56.3, $n=9$), 57–62 in ϕ (mean 59.1, $n=4$); IPSB 35–39.3% (mean 36.7%, $n=13$) of TW; posterior dorsal elytral spines diverging, IPSA 118.2–155.6% (mean 137.1%, $n=13$) of IPSB, with ϕ values slightly less than δ (118.2–135.7% vs 125–155.6%); IAPSB 19.4–24.6% (mean 20.9%, $n=12$) of TW; post-humeral spine well developed with tip strongly reflexed caudad. Legs with femora moderately swollen; tibial teeth small; corbels moderately narrow, without scales and with 9–15 adventitious setae. Venter of δ with post-coxal groove and bead-like granules on ventrite 1.

Vestiture intraspecifically constant, with scale and setal coloration and configuration as follows: white scales (with pearly reflections) and black-bronze scales dense, imbricate-appressed; pink-brown scales (with coppery reflections) dense, imbricate-semi erect; blue scales sparse/tessellate-appressed; setae dark brown, prominent, hair-like, semi-erect to recumbent, scattered evenly over antennae, legs and body (including elytral spines). Underside throughout (including head) with white scales. Eyes encircled with white scales; dorsal remainder of head and rostrum with white scales except for narrow median vitta of bronze to black-bronze scales and some bronze scales behind eyes. Prothorax dorsally with moderately broad median vitta of white scales flanked by two slightly broader longitudinal admedian tracts of black-bronze scales which cover everything except the deeper grooves; these dark tracts each contain a small mid-lateral and baso-lateral patch of white and/or blue scales, as well as scattered blue scales at anterior margin which do not reach median vitta; sides with white scales. Elytra with a white sutural vitta covering width of interstria 1 and

1.

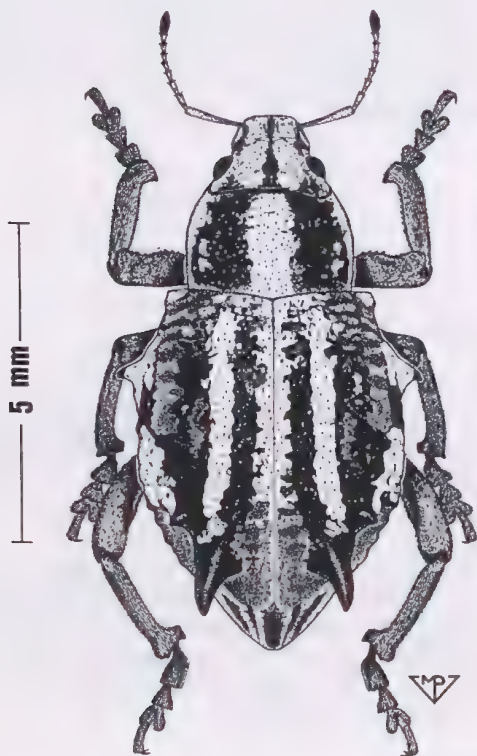


Figure 1 Dorsal view of *Catasarcus militaris* holotype.

extending from base to just anterior of anterior dorsal spine level, expanding at elytral base to form narrow transverse line reaching from suture to third stria; a black-bronze vitta covering width of interstria 2 and extending from near elytral base onto base of posterior dorsal spines, also with narrow white vitta (sometimes broken up into series of spots) covering lateral half of caudal 2/3 of interstria (to posterior dorsal spine) in some southern specimens; a very pronounced and dense white vitta covering width of interstria 3 and extending from near elytral base onto base of posterior dorsal spines; interstria 4 vestiture, for distance between elytral base and posterior dorsal spine, as follows: basal 1/4 uniformly pink-brown for interstitial width, following 3/8 with an indistinct line of pink-brown scales (containing interspersed black-bronze scales), caudal 3/8 (to level of posterior dorsal spine) covered in black-bronze scales; medial half of interstria 5 with pink-brown scales for basal 1/4 distance between elytral base and posterior dorsal spines, with remaining 3/4 bronze-black to anterior dorsal spine; interstria 6 and lateral half of interstria 5 with pink-brown scales covering respective widths for basal 5/8 distance between elytral base and posterior dorsal spines, thereafter interrupted by diagonal line of white scales reaching from humeral tubercle onto base of anterior dorsal spine; elytral sides white below a line which reaches from humeral tubercle (at elytral base) to anterior dorsal spine, thereafter angling down to just posterior of hind coxae at level of top of post-humeral spine, and finally angling slightly up and around to posterior declivity of elytra; white elytral sides containing a black spot just dorso-caudal to post-humeral spine and just ventral to line between humeral tubercle and anterior dorsal spine; elytra with pink-brown scales anterior to and below post-humeral spine; scales at dorsal 3/8 of posterior declivity pink-brown for elytral width, extending dorsally between posterior dorsal spines to level of anterior dorsal spines; ventral 5/8 of posterior declivity (to elytral apex) white with five apically converging, separate black-bronze vittae which, together, dorsally cover the same elytral width as the distance between the posterior dorsal spines. Legs covered in white, bluish and bronze scales, with blue scales on femora particularly prominent; adventitious corbellar setae brown, hair-like. Antennal scape with bronze and white scales, funicle segments mostly white.

Ovipositor with valves apically explanate/flattened and blade-like. Aedeagus as in figure 2.

Distribution

At present, known only from two localities (26°32'S, 113°59'E and 27°23'S, 114°14'E) near mid-west coastal Western Australia.

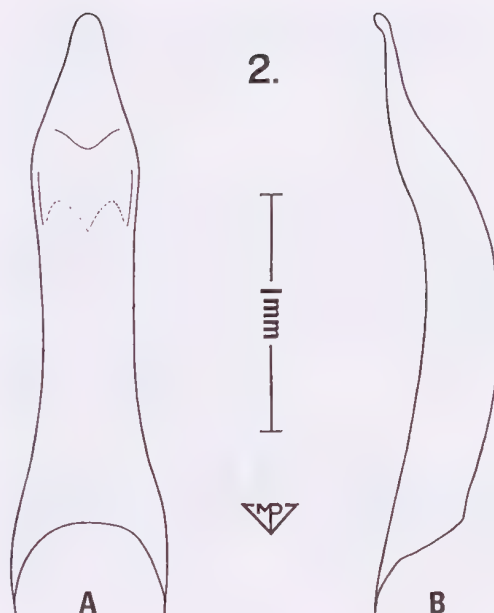


Figure 2 Aedeagus of *Catasarcus militaris*: A, dorsal view; B, left lateral view.

Remarks

On the basis of similarity in size, general shape and morphology, vestiture pattern and ovipositor structure, I believe that *C. militaris* is most closely related to three quadrispinate species: *C. albisparsus* Pascoe, 1870; *C. cicatricosus* Pascoe, 1870; *C. marginispinis* Pascoe, 1870. The latter three species are herein informally referred to as the *C. marginispinis* species-group, which may be diagnosed with respect to other quadrispinate *Catasarcus* by the presence of small forwardly-directed tubercles at elytral base. *C. militaris* differs from the *C. marginispinis* species-group as follows: it lacks the small forwardly-directed tubercles at elytral base; in both sexes, its anterior dorsal elytral spine length is relatively shorter than and non-overlapping with this group (LAS 0–56% of LPS vs >59% of same); in both sexes, its anterior dorsal spines are set more caudad on elytra than those of the latter group (ASI: 50–58 vs 44–54). Indeed, among the quadrispinate *Catasarcus*, *C. militaris* has the shortest anterior dorsal spines known (to the point where they are absent in the northern ♂ paratype). *Catasarcus militaris* further differs from *C. marginispinis* (ASI: ♂, 44–49; ♀, 47–53) as follows: non overlapping ♂ ASI; weakly vs strongly sexually dimorphic ASI; lateral frontal carinae (on head) present vs absent; median rostral carina parallel to frons vs arched. *Catasarcus militaris* also differs from *C. albisparsus* (ASI: ♂, 48–53; ♀, 49–53)

and *C. cicatricosus* (ASI: ♂, 47–54; ♀, 47–53) by its more colourful and strongly defined vestiture, and further differs from *C. albisparsus* by having more adventitious corbellar setae (9–15 vs 2–10) and from *C. cicatricosus* by the following: details of ovipositor structure (see Thompson, 1968:440); median rostral carina parallel to frons vs arched; posterior dorsal spines set less caudad (PSI: 52–62 vs 59–66) on elytra, in both sexes; strongly vs weakly sexually dimorphic PSI. *Catasarcus militaris* appears to have a more northern distribution than these three species and all four taxa are apparently allopatric (Figure 3).

It has been suggested (anonymous referee's comments) that *C. militaris* may be related to *C. intermedius* Pascoe, 1870, with which it shares similarly placed dorsal elytral spines (the two species have the highest ASI values among described species in the genus) and multisetose corbels. *Catasarcus militaris* may be differentiated from *C. intermedius* (prothorax length to width ratio, 10 : 16.3–17.9; PSI: ♀ 63.7–70.4, ♂ 58.0–63.0; IPSB/TW: ♀ 30.4–35.7, ♂ 28.6–32.7) as follows: prothorax narrower; posterior dorsal spines set less

caudad on elytra (non-overlapping ranges of PSI for ♀, minimal overlap for ♂); IPSB/TW higher (non-overlapping ranges for both sexes; apparently due to a more gracile general form); less numerous corbellar setae; elytral pattern more colourful, bolder and longitudinally aligned (vs white/pearly scales only, less densely distributed and forming an indistinct oblique white/pale line (from post-humeral spine to just anterior of anterior dorsal spine) on each elytron); apparently allopatric distributions (Figure 3).

I collected the three northern *C. militaris* types, at 1345–1445 hrs (Western Standard Time), on the topmost leaves (1–2.5 metres above ground) of mature non-flowering *Grevillea candelabroides* Gardner growing on the swale and crest of a red sandridge. The sandridge was well vegetated with *Grevillea*, *Hakea*, *Banksia*, *Eucalyptus* (mallee), *Calothamnus* and *Plectrachne* species. Conditions were hot (circa 40° C) with no wind, and the weevils were active, though evidence of feeding was not found. They were found sympatric, but not syntopic, with only one other *Catasarcus* species, *C. carbo* Pascoe, 1870 (northern form). The Carrollgouda Well specimens of *C. militaris* are without associated ecological data. However, *C. carbo* (northern form) has also been recorded from the latter locality, suggesting a possible ecological/distributional association between these two taxa. *Catasarcus carbo*, a quadrispinate species, is distinguished from *C. militaris* by its larger size, squamose corbels, rugose pronotal disc, weak to obsolete postocular lobes, more convex eyes and anterior dorsal spines set less caudad on elytra (ASI: 43–54) in both sexes, with the "northern form" also possessing less distinct, more sparsely distributed setae and an elytral pattern of metallic golden scale patches (covered in bright yellow powdery exudate in live specimens) forming an oblique (not longitudinal) marking/tract (from post-humeral spine to anterior dorsal spine) on each elytron.

Etymology

The specific epithet, Latin for military, alludes to the vestiture pattern and coloration of this attractive taxon, which approximates that of many early (18th and 19th century) military uniforms.

Additional Material Examined

C. albisparsus: **Australia: Western Australia:** 1 ♀, Burma Road Reserve, 30 km E. of Walkaway, 4 September 1987, R.P. McMillan (WAM); 1 ♀, Watheroo Nat. Park (30°12'S, 115°50'E), 16–17 May 1981, B. Hanich and T.F. Houston 384 a–b (WAM).

C. cicatricosus: **Australia: Western Australia:** 1 ♀, 16 km NW. of Eneabba (29°49'S, 115°16'E), 9–12 September 1987, T.F. Houston 652 (WAM); 6 ♀, 3

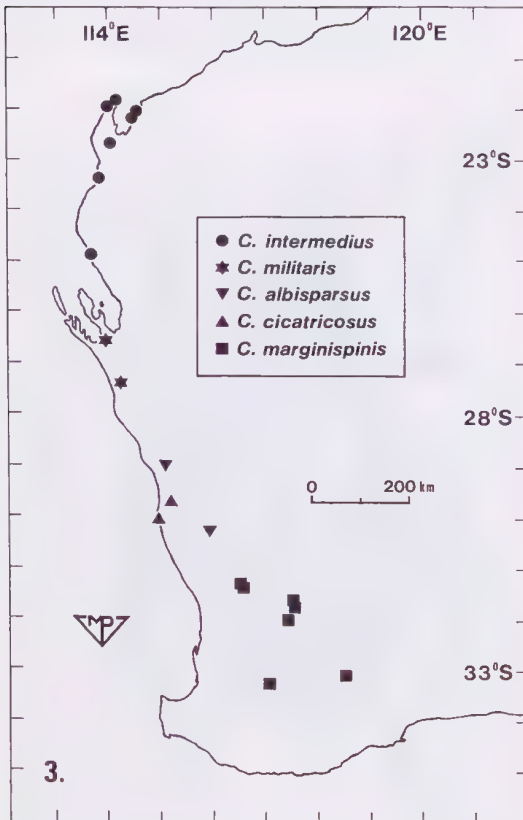


Figure 3 Collection localities for five Western Australian *Catasarcus* species mentioned in text.

♂, Greenhead, 2 September 1981, R.P. McMillan (WAM).

C. marginispinis: **Australia: Western Australia:** 1 ♀, 1 ♂, Bejoording, October 1951, R.P. McMillan (WAM 53/996,992); 1 ♀, 5 m[iles] N. of Wagin Turnoff, 9 April 1971, F.H. Uther Baker (WAM); 6 ♀, 2 ♂, Watterning, 27 August 1950, R.P. McMillan (WAM 50/4535–7, 51/1440–4); 1 ♀, 1 ♂, same data except February 1950 (WAM).

C. intermedius: **Australia: Western Australia:** 1 ♀, 1 km W. of Bullara HS, 20 July 1994, D. Knowles (MPWA); 3 unsexed specimens, Hope Island, 21 April 1990, A. Williams (CALM); 10 ♀, 9 ♂, North-West Cape, 25 July 1963, A.M. Douglas (WAM 65/4–6, 8, 10–13, 17–18, 20–22, 27, 30, 33, 417–419); 1 ♂, North-West Cape, Yardie Creek, 9 December 1978, D. Knowles and M. Hanlon (WAM); 1 unsexed specimen, Tent Island, 23 April 1990, A. Start (CALM); 1 ♀, 8.4 km N. of Warroora HS, 31 May 1988, M. Peterson (MPWA); 1 ♂, Yardie Creek, Cape Range, 21 January 1969, D.D. Guilani (WAM).

C. carbo (northern form): **Australia: Western Australia:** 1 ♀, 8.5 km NE. of Tamala HS, 10 December 1988, M. Peterson (MPWA); 1 ♀, 37.8 km

NE. of Tamala HS, 10 December 1988, M. Peterson (MPWA); 1 ♀, 3 ♂, Carrollgouda Well, 30 November 1968, Hale School (WAM); 1 ♀, 1 mile E. of Gee Gie, Kalbarri area, 26 November 1968, Hale School (WAM).

ACKNOWLEDGEMENTS

I thank Dr G.M. Shea (Sydney) and Ms B.M. Coulson (Perth) for assistance with typing of the manuscript and critical comment; Dr T.F. Houston and Mr B. Hanich (WAM), and Dr G. Friend (CALM), for access to specimens in their care and use of equipment; two anonymous referees for critical comment.

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Manuscript received 11 October 1994; accepted 21 November 1994.

Australites from Earraheedy Station, Western Australia with notes on australites from the nearby Glenayle Station

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Abstract – Australites from Earraheedy Station totalling 8720 specimens have been classified morphologically and compared with australites from the Eastern Goldfields centred 500 km to the south. The only major difference is the high percentage (15.4%) of flakes and flaked cores in the Earraheedy specimens arising from widespread destructive use of australites by Aborigines, though the percentage has been inflated by the manner of collection of the sample. A much smaller and unrepresentative sample of 334 specimens is available from the nearby Glenayle Station. Australites were less abundant than at Earraheedy Station but at least equally popular as artifact material. Considerations of specific gravity suggest that they are of the “normal australite” chemical type of Chapman (1971).

INTRODUCTION

Earraheedy Station is centred 25°40'S, 121°49'E in the northeastern corner of the Salt Lake Division of Western Australia (Jutson 1934) and near the geographical centre of the state. The station has a semi-arid climate with large temperature fluctuations and internal drainage to salt lakes and claypans.

Access to additional or enlarged private collections of australites from Earraheedy Station has increased the available sample from 2208 to 8720 specimens, thus enabling the upgrading of an earlier statement (Cleverly 1991). Contributions to the supplemented sample are: Western Australian Museum 57, Western Australian School of Mines 1578, A. Quadrio 244, M.K. Quartermaine family 1742, C. Strugnell 51, L.P. Strugnell 4706, T. Wilks 314, C. Ward and others 28. A further 148 australites in the Smithsonian Institution collection (Chalmers *et al.* 1976) and the highly biased W.A. School of Mines item 11597 of 175 specimens were not included in the sample.

DISTRIBUTION AND RECOVERY OF AUSTRALITES

The find sites of 85% of the australites are known, though not all with precision (Figure 1). Nearly 39% of the sample was found by station staff incidentally to their station duties or in subsequent searches of sites already found to be productive. Private and commercial collectors found the other 61% of the sample.

Australites are present on much, probably all, of the station (M.K. Quartermaine, pers. comm.). The

zone of proven occurrence trending southeast from the homestead (Figure 1) is coincident with present station occupancy and activity except for the contributions from private and commercial collectors, especially at the southeastern end of the zone, where australites are unusually abundant.

Some of the australites are closely associated with natural water sources formerly used by Aborigines. The australites found at those sites include numerous flakes and flaked cores. Akerman (1975) identified 93 struck flakes, 27 cores, 23 used flakes and 50 tools, a total of 193 artifacts or 16.4% of the 1179 Earraheedy australites in the Western Australian School of Mines collection in 1975, but omitting the biased catalogue item 11597 which is considered elsewhere below. The identification of australite flakes in other collections as artifacts is suggested by their association with flakes of chert and other siliceous rocks around natural sources of drinkable water.

The sites of abundant australite occurrence include Pope Claypan (136 australite flakes and flaked cores/308 australite specimens); Spider Bore with nearby water hole (129/740); Neville Claypan (37/66); Hamilton Claypan (50/90); an area south and southeast of Hegarty Bore including the freshwater Tommy Lake (474/4707). The list could be extended by citing minor recoveries e.g., the claypan south of Ian Bore (8/24). The only figures available for other basins are 11/314 or only 3.5% flakes for australites collected by T. Wilks from two small basins described as “salt lakes” in the eastern part of the station. Australites were probably brought to the water sources from the immediately surrounding country but there was no need for

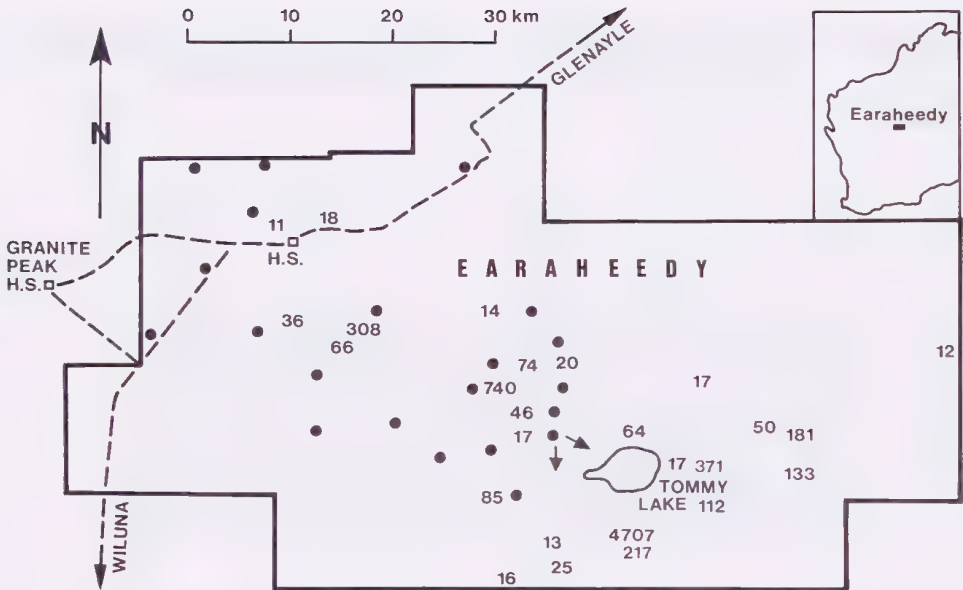


Figure 1 Map of Earaaheedy Station showing numbers of australites at their find sites. Small filled circles represent 1–10 australites. The provenance of the Strugnell collections of 4757 specimens to the “south and southeast of Hegarty Bore” is shown diagrammatically by arrows. The parcels of 36 and 112 australites are in the Smithsonian Institution collection and are not part of the sample examined.

them to be imported from outside the station because un-flaked specimens greatly predominate in all collections contributing to the sample.

AUSTRALITE FEATURES AND SHAPES

Some of the considerable variety of features shown by 21 of the 34 shape types in the Earaaheedy material are shown in Figures 2 and 3. Examples of small bowls, of which there are 65 in the sample, have been shown previously (Cleverly 1973); likewise, for examples of the 106 aberrant specimens, see Cleverly (1982). Two circumferentially spalled specimens, perhaps heated suddenly in grass fires, have been figured by Cleverly (1990, figure 3).

Some of the australites on Earaaheedy Station were subjected to abrasion, especially by blown sand (Figures 2W, X; 3E, F). As a result of weathering, especially temperature changes, australites were degraded through a series of shapes (Cleverly 1986, figure 3). In this series, indicators II are especially well represented at Earaaheedy (Figures 2C, M, DD; 3D, H, O). Etching by the chemicals in soil water to produce pits and sawcuts (Figure 2B–F, T, DD–GG) is also evident though Earaaheedy Station now has a generally dry, sub-arid climate. V-grooves relieving residual strains (Figure 2U) and U-grooves (Figure 2K, O)

are etched on the posterior surfaces of larger cores, and less commonly, U-grooves are etched upon anterior surfaces created by loss of the stress shells.

No australite weighing more than 100 g is present though Earaaheedy Station is marginal to the western of two sectors of occurrence of such specimens (Cleverly and Scrymgour 1978). The heaviest Earaaheedy australite is a naturally broken broad oval core weighing 68.6 g or c. 73 g prior to artificial damage. There are 165 australites (1.9% of sample) of weight 10 g or more, about the same abundance as for Hampton Hill Station in the Eastern Goldfields (394 such specimens, or 1.8% of the 22 307 australites).

A notable feature of the Earaaheedy australites is the high number of them – 9043 in collections inclusive of the 323 left out of the sample, and an unknown number sold to lapidaries and mineral dealers. One of the excluded items is W.A. School of Mines catalogue No. 11597 comprising 175 specimens rejected from a parcel offered for sale. Akerman (1975) identified 116 artifacts (struck flakes, used flakes, tools, cores) in this rejected material. A parcel of average constitution would have included several hundred additional unflaked australites. Amongst Western Australian localities, only Hampton Hill Station has a higher representation in collections.



Figure 2 Australites from Earraheedy Station, Western Australia. ps signifies posterior surface of flight, se side elevation, ee end elevation. In elevational views, direction of flight is towards bottom of page. Scale in centimetres and millimetres. A: ps of round indicator I. B: ps of lens distorted by sawcuts. C and D: ps and se of round indicator II. E and F: Major surface and side view of round indicator II, orientation uncertain. G: se of faceted round core. H: as of faceted round core. I: se of stopper type round core. J: se of round core with ovoid "flake" scars. K: se of round core. L: ps of broad oval lens losing stress shell along sawcuts. M and N: ps and ee of broad oval indicator II. O: ps of broad oval core. P and Q: ps and se of narrow oval canoe, one end lost. R and S: ps and ee of narrow oval lens with stubs of flange. T: as of narrow oval lens with transverse sawcut. U and V: ps and se of narrow oval core. W and X: ps and se of tapering narrow oval core with remnants of "flake" scars. Y: as of wedged narrow oval core. AA and BB: ps and se of abraded boat-lens ex canoe. CC: ps of flanged dumbbell, incomplete. DD and EE: ps and as of boat-indicator II. FF and GG: ps and as of boat-indicator II.

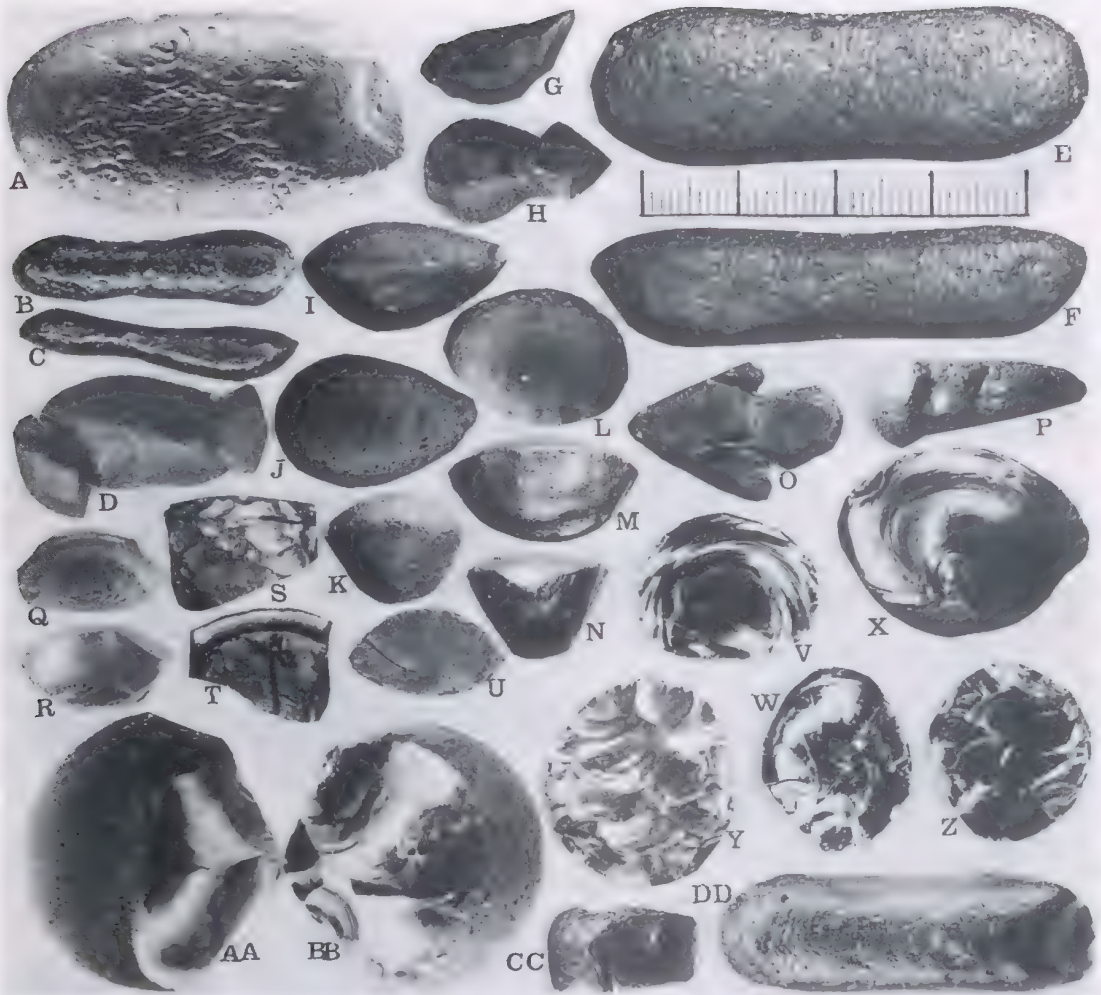


Figure 3 Australites from Earahedy Station, Western Australia. ps signifies posterior surface of flight, as anterior surface, se side elevation, ee end elevation. In elevational views, direction of flight is towards bottom of page. Scale in centimetres and millimetres. A: ps of boat-core broken through bubble crater. B and C: ps and se of dumbbell-lens. D: as of half-dumbbell indicator II. E and F: ps and se of abraded dumbbell-core. G: se of teardrop-lens. H: as of teardrop-indicator II. I, J and K: se, ps and ee of teardrop-core. L, M and N: ps, se and ee of conical core. O: as of broken elongate indicator II, so-called "trilobite". P: se of broken elongate indicator II, "club" form. Q and R: flow-ridged outer and spalled inner surfaces of fragment of stress shell. S and T: flow-ridged outer and spalled inner surfaces of composite flange-stress shell fragment. U: Broken lens-form losing stress shell along sawcuts. V: Flake. W: Flake with radial percussion ribbing. X: Flaked core. Y: Worked flake. Z: Worked flake. AA and BB: Two views of a pointed australite tool. CC: Small chisel-shaped tool ex elongate indicator II, other side similar. DD: Chisel-shaped tool ex stout-waisted dumbbell-core, other side closely similar.

COMPARISON BETWEEN AUSTRALITES FROM EARAHEEDY STATION AND FROM THE EASTERN GOLDFIELDS

The sample was classified morphologically and extracts from the classification with weight data are presented in Table 1 using the system and procedure of Cleverly (1986). The mean values and standard deviations for eight samples from the

Eastern Goldfields centred about 500 km to the south are also given in Table 1. A comparison is made because both Earahedy Station and the Eastern Goldfields have an arid to sub-arid climate and internal drainage, and are within the field of occurrence of the "normal australite" chemical type (Chapman 1971).

The only major difference between the Earahedy

Table 1 Comparison between australites from, 1, Earaaheedy Station (this work) and, 2, eight samples from the Eastern Goldfields of Western Australia, mean and standard deviation (Cleverly 1994).

		2		
		1	Mean	S.D.
1	Whole forms or essentially so %	29.8	38.2	9.5
2	Incomplete but classifiable %	11.4	12.8	2.2
3	Total classifiable %	41.2	51.0	9.8
4	Fragments and indeterminate %	43.4	47.9	9.9
5	Flakes and flaked core %	15.4	1.1	1.1
6	Round forms %	69.7	69.0	7.9
7	Broad oval forms %	11.1	8.2	3.5
8	Round plus broad oval forms %	80.8	77.2	4.6
9	Narrow oval forms %	6.9	7.6	2.0
10	Boat forms %	2.5	5.1	0.8
11	Dumbbell forms %	6.0	7.2	1.5
12	Teardrop forms %	3.8	3.0	1.7
13	Aberrant forms as a percentage of classifiable	2.9	3.0	0.9
14	Flanged, disk and plate, bowl and canoe forms %	2.7	2.4	3.0
15	Indicators I %	0.8	1.7	1.4
16	Lens-forms %	53.1	60.4	11.1
17	Indicators II %	2.4	1.2	1.1
18	Cores including conical %	41.0	34.2	11.0
19	Cores/lens-forms ratio	0.77	0.61	0.27
20	Number of whole australites	2599		
21	Mean weight of whole australites (g)	3.30	2.75	1.07
22	Total number of specimens	8720		
23	Mean weight of all specimens (g)	2.10	1.87	0.57
24	Number of shape types in sample	34		

and the Eastern Goldfields australites is the high percentage of flaked specimens – 15.4% at Earaaheedy, 1.1% in the Goldfields (Table 1, item 5). The abundance of flaked australites collected at sites over a length exceeding 50 km is unique in the writer's experience. In the Mount Remarkable-Yerilla portion of the Eastern Goldfields, about one third of the available specimens were flakes, but they were from a single water source (Cleverly 1988). The use of australites at Earaaheedy appears to have been general, at least throughout the area which is well represented in the sample. Flakes and flaked cores constitute 28.4% of the 1319 australite specimens collected from fresh water claypans, and because collectors returned continually to those productive sites, the abundance of flakes in the overall sample (15.4%) is a slightly inflated figure.

A minor difference between the Earaaheedy and Eastern Goldfields samples is the low percentage of boat forms – 2.5% compared with 5.1% (Table 1, item 10).

The mean weight of 3.30 g for whole australites is within the usual range of 2.75 ± 1.07 g for those

of the Eastern Goldfields (Table 1, item 21); similarly, the mean weight of 2.10 g for all specimens conforms with 1.87 ± 0.57 g for the Eastern Goldfields (Table 1, item 23).

Thirty four shape types are present in the sample, a figure within the range c. 28 – 40 for an Eastern Goldfields sample of comparable size (Cleverly 1994).

CONCLUSION

Australites from Earaaheedy station are similar in major features to those of the Eastern Goldfields except in the abundance of flaked specimens, and that is an artificial feature resulting from their destructive use by Aborigines.

NOTES ON AUSTRALITES FROM GLENAYLE STATION

Glenayle Station is north of Earaaheedy Station with much of the intervening country unoccupied (Figure 4). The following australites found on Glenayle Station were available for examination.

1. Twenty specimens from the claypan 1 km east of the homestead (Western Australian School of Mines collection).
2. Ms J. Ward's collection of 257 australites from places as far west as Scorpion Bore (67 km west-northwest of the homestead and on the Canning Stock Route) to near the eastern boundary and to within a few kilometres of the far northern boundary. A major, but indistinguishable and unspecified, component of this collection was gathered meticulously from the claypan 1 km east of the homestead. The numerous small flakes in this component are responsible for the unusually low average weight of 1.05 g for the collection. Australites are known to the Ward family as "moppins" from an Aboriginal word, probably a

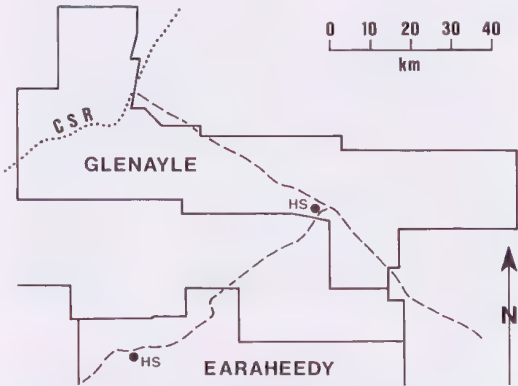


Figure 4 Map showing location of Glenayle Station relative to Earaaheedy Station. CSR signifies Canning Stock Route.

variant or corruption of "mappin", meaning "emu stones", a word used by Aborigines for australites in Western Australia (Baker 1957). Emus frequently use australites as gizzard stones (Fenner 1949).

3. Mr H.W. Ward's collection of 39 australites, most found singly at points throughout the station during his 46 years of occupation. These more obvious specimens were collected casually, not as a result of intended search and have the very high average weight of 6.95 g.

4. Eighteen specimens found by W.H. and E.I. Cleverly during a brief reconnaissance of the central part of the station. Two australite flakes were found in claypans west of Sunday Well, 31 km eastnortheast of the homestead. Fifteen flakes/flaked cores and one whole specimen (probably too small for use) were found on the slope overlooking Jilca Soak from the south, 8 km west of the homestead. Flakes of chalcedony, quartzite and other siliceous materials were plentiful at the recovery sites and broken grinders and base stones were especially abundant at Jilca Soak. No australites were recovered during any of 20 brief searches at a distance from sources of fresh water, though other flaked materials were ubiquitous.

The 334 australites have general morphological classification:

Whole forms or essentially so	57
Incomplete but classifiable	31
Total classifiable (Cleverly 1986)	88
Fragments and indeterminate	66
Flakes and flaked cores	180

All four units in the sample contain flakes or flaked cores, which constitute 54% of the sample in contrast to the mean 1.1% in Eastern Goldfields samples (Table 1, item 5). A detailed statement using the classification and procedure of Cleverly (1986) is inappropriate because most items of the Table would be based upon 88 or fewer specimens. Moreover, there is bias of location and/or australite size in all four units in the sample. However, some general conclusions are possible.

Australites are (or were) sparsely but widely present over much of Glenayle Station. They were popular with Aborigines as artifact material and are now present largely as flakes and flaked cores in or around the sources of fresh water. When considered in conjunction with the collections from Earahedy Station, it is likely that the destructive use of australites was prevalent over a very large area with a northsouth dimension of more than 80 km, though abundant alternative materials were available.

Specific gravities were determined for 100 australite specimens representing proportionally all four units in the sample. The frequency polygon of specific gravity with a single strong mode in the 2.45–2.46 interval and lack of values exceeding 2.47

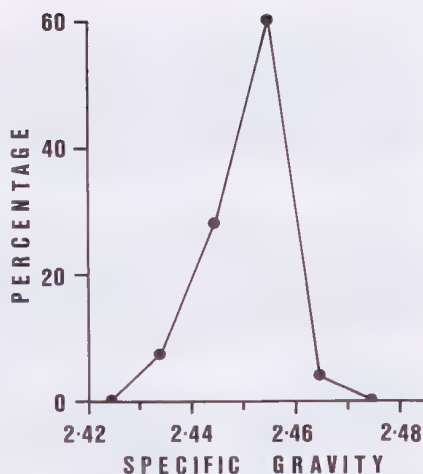


Figure 5 Frequency polygon of specific gravity at 0.01 unit intervals for 100 australites found on Glenayle Station, Western Australia.

(Figure 5) is typical of the "normal australite" chemical type which is present also at Earahedy Station (Chapman 1971).

ACKNOWLEDGEMENTS

I thank Mr M.K. Quartermaine and Mr R.A. Quartermaine of Earahedy Station for their book-keeping of australite recoveries and numerous courtesies, and Mr and Mrs H.W. Ward of Glenayle Station for generous hospitality and assistance. Additionally to the above persons, the following kindly lent australites and/or provided information: Messrs A. Quadrio, L.P. Strugnell, Chris Ward, Ms J. Ward, Mr and Mrs L.W. Ward, Mr T. Wilks. Ms J.M. Wearne drafted Figures 1, 4 and 5. Mr M.K. Quartermaine processed my photographs used in Figures 2 and 3. Evelyn Cleverly and June Emerson typed the manuscript and the corrected copy.

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Manuscript received 13 September 1994; accepted 21 December 1994.

A new species of Cardinalfish (*Apogon*: Apogonidae) from northwestern Australia

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Abstract – A new species of apogonid fish of the genus *Apogon* is described from the Northern Territory and northern Western Australia. *Apogon unitaeniatus* is described on the basis of 94 trawl-captured specimens from Darwin Harbour and Shoal Bay in the Northern Territory, and the Kimberley coast of Western Australia. It is a member of the subgenus *Pristiapogon* and very similar in appearance to *A. abrogramma* Fraser and Lachner of the Indo-West Pacific. Both species are distinguished by a blackish midlateral stripe. However, they are readily separated on the basis of counts for gill rakers and pectoral rays (22–25 and 15 respectively for *A. unitaeniatus* versus 17–19 and 13 for *A. abrogramma*).

INTRODUCTION

Cardinalfishes of the family Apogonidae are one of the most abundant groups of tropical reef fishes. They are primarily nocturnal, although readily observable during daylight when they shelter in caves and crevices or around coral formations. The generic classification of Apogonidae was reviewed in detail by Fraser (1972), but a knowledge of the species composition is still incomplete. Fraser recognized 19 genera. The estimated number of species in the family is 230–250. At least half of the species occur in the area comprised of New Guinea, northern Australia, Indonesia, and the Philippine Archipelago.

The present paper describes a new species of the genus *Apogon* first collected by a prawn trawler off the Kimberley coast of Western Australia in 1978. The specimens were subsequently deposited at the Australian Museum and were recognised in 1992 during an examination of the institution's apogonid holdings. Additional specimens were procured during dredging operations by Rex Williams of the Northern Territory Museum during 1993.

Type specimens of the new species are deposited at the Australian Museum, Sydney (AMS), Northern Territory Museum, Darwin (NTM), and the Western Australian Museum, Perth (WAM).

Lengths given for specimens are standard length (SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of hypural plate); body depth is the maximum depth from the base of the dorsal spines; body width is measured just posterior to the gill opening; head length is taken from the front of the upper lip to the end of the opercular membrane, and snout length from the same anterior point to the fleshy edge of the

orbit; orbit diameter is the greatest fleshy diameter, and interorbital width the least bony width; caudal peduncle depth is the least depth, and caudal peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and soft rays are measured to their extreme bases; caudal concavity is the horizontal distance between verticals at the tips of the shortest and longest caudal-fin rays.

Pectoral-ray counts include the upper rudimentary ray; lateral-line scale counts are made to the base of the caudal fin (hence do not include the scales posterior to the hypural plate); gill-raker counts are made on the first gill arch; the count of the upper-limb rakers is given first, followed by the lower-limb count; the raker at the angle is contained in the lower-limb count.

Proportional measurements of type specimens are given in Table 1 as percentages of the standard length. Data in parentheses in the description refer to paratypes.

TAXONOMY

Apogon unitaeniatus sp. nov.

Figure 1

Holotype

AMS I.20402–036, 50.2 mm SL, off NE portion of Bonaparte Archipelago, northern Western Australia (approximately 14°00'S, 124°45'E), 12–60 m, prawn trawl, C. O'Conner, April 1978.

Paratypes

AMS I.20402–000, 50.5 mm SL, collected with

Table 1 Proportional measurements of type specimens of *Apogon unitaeniatus* expressed as percentage of the standard length (* denotes damaged fins).

Character	Holotype		NTM		Paratypes		NTM	
	AMS		NTM		AMS	NTM	WAM	NTM
	I.20402 -036	S.13711 -008	S.13711 -008		I.20402 -000	S.13711 -008	P.30743 -001	S.13711 -008
Standard length (mm)	50.2	57.6	51.8		50.5	48.2	47.6	47.0
Body depth	39.6	36.3	36.9		39.0	35.3	36.8	36.6
Body width	16.9	17.2	16.0		17.0	15.4	17.0	16.4
Head length	40.8	42.0	40.9		42.6	38.2	41.0	39.4
Snout length	10.8	9.2	8.1		10.3	9.1	8.4	9.4
Orbit diameter	13.9	12.7	12.7		12.5	12.0	12.2	13.2
Interorbital width	10.0	9.5	9.7		9.1	9.1	9.0	9.4
Upper jaw length	21.1	21.2	21.6		20.8	20.3	20.0	21.9
Caudal peduncle depth	14.7	16.1	16.4		15.4	14.7	13.7	14.5
Caudal peduncle length	24.7	25.7	24.7		23.2	28.4	25.6	25.5
Predorsal length	46.2	41.1	40.9		44.2	40.9	41.4	41.5
Preanal length	65.3	65.1	64.1		66.3	64.3	63.7	65.5
Prepelvic length	38.0	39.6	40.3		40.6	37.6	40.5	38.3
Length 1st dorsal spine	1.8	1.9	2.7		3.0	2.1	2.3	2.1
Length 2nd dorsal spine	7.8	5.7	6.6		7.7	7.1	8.0	7.0
Length 3rd dorsal spine	17.5	16.3	16.0		18.6	17.6	17.6	17.7
Spine of 2nd dorsal	15.9	15.6	13.3		13.3	13.2	13.2	13.2
Longest dorsal ray	*18.9	26.9	26.4		16.8	25.9	*21.8	23.4
Length 1st anal spine	3.4	2.3	3.3		3.4	2.7	2.3	3.8
Length 2nd anal spine	8.8	14.1	14.1		12.1	13.7	14.1	12.8
Longest anal ray	*14.1	22.6	23.0		*15.4	22.4	*19.1	21.1
Caudal fin length	*21.9	35.1	32.6		*24.9	36.1	*22.4	34.5
Caudal concavity	*3.9	9.7	9.7		*2.9	11.6	*7.5	8.5
Pectoral fin length	*6.1	25.9	27.0		*7.1	24.9	24.4	26.6
Pelvic spine length	15.1	14.9	13.9		15.4	15.1	14.3	14.5
Pelvic fin length	17.7	24.0	22.8		20.8	23.2	22.7	22.3

holotype; NTM S.13706-007, 15 specimens, 23.5–57.7 mm SL, middle of Fannie Bay, Darwin Harbour, Northern Territory (approximately 12°25.6'S, 130°49'S) 3–4 m, R. Williams, 7 July 1993; NTM S.13707-002, 9 specimens, 23.6–36.2 mm SL, north of Talc Head, Darwin Harbour (approximately 12°27.8'S 130°46'S), 2 m, R. Williams, 8 July 1993; NTM S.13711-008, 60 specimens, 17.8–57.7 mm SL, off Mila Beach, Darwin Harbour (approximately 12°29.6'S, 130°46.5'E), 1–2 m, R. Williams, 8 July 1993; NTM S.13721-006, 50.5 mm SL, south of Mitchell Creek, Darwin Harbour (approximately 12°30.9'S, 130°56.4'E), 7 m, R. Williams, 16 July 1993; NTM S.13723-003, 3 specimens, 27.9–28.7 mm SL, mouth of Hudson Creek, Darwin Harbour (approximately 12°29.3'S, 130°55.4'E), 2 m, R. Williams, 16 July 1993; NTM S.13732-001, 52.5 mm SL, north of Lee Point, Shoal Bay, Northern Territory (approximately 12°16'S, 130°54'E), 17 m, R. Williams, 16 March 1993; NTM S.13735-011, 33.3 mm SL, West Arm, Darwin Harbour (approximately 12°33.3'S, 130°46.7'S), 12 m, R. Williams, 9 September 1993; NTM S.13813-001, 36.0 mm SL, north end of Shoal Bay, Northern Territory (approximately 12°13'S, 130°56'S), 13 m, R. Williams, 12 October 1993; WAM P.30743-001, 47.6 mm SL, collected with holotype.

Diagnosis

A species of the subgenus *Pristiapogon* with the following combination of characters: dorsal rays VII–I,9; anal rays II,8; pectoral rays 15; lateral-line scales 24; predorsal scales 4; gill rakers 7–9+15–16, including 1–2 rudiments at beginning of upper and lower limbs; fine serrae present on margin of preopercle, preopercular ridge, and circumorbitals; body depth 2.5–2.8 in SL; colour entirely whitish except for dark midlateral stripe extending from upper edge of preopercle to base of caudal fin.

Description

Dorsal rays VII–I,9; anal rays II,8; all dorsal and anal soft rays branched, the last to base; pectoral rays 15, the uppermost and lowermost pairs unbranched; pelvic rays I,5, all rays branched; principal caudal rays 17, the upper and lowermost rays unbranched; upper and lower precurrent caudal rays 6, the most posterior segmented; lateral-line scales 24, plus 5 pored scales posterior to hypural plate, the last narrow, somewhat triangular; scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales 4, the fourth notched posteriorly to accommodate origin of first dorsal fin; circumpeduncular scales 11; gill rakers 7+15 (7–9+15–16), including 1–2 rudiments at

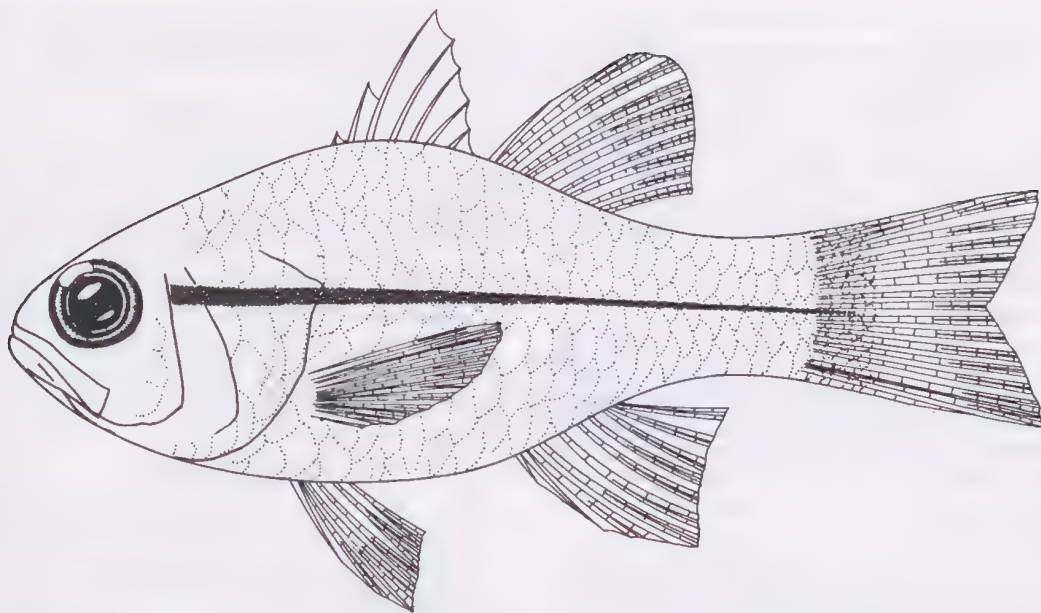


Figure 1 Drawing of holotype of *Apogon unitaeniatus*, 50.2 mm SL. Damaged fins are reconstructed.

beginning of upper and lower limbs; branchiostegal rays 7; vertebrae 10 + 14.

Body depth 2.5 (2.6–2.8) in SL; body width 2.3 (2.1–2.3) in depth; head length 2.4 (2.3–2.6) in SL; dorsal profile of head straight except for rounded front of snout; snout length 3.8 (4.2–5.0) in head; eye diameter 2.9 (3.0–3.4) in head; interorbital width 4.1 (4.2–4.7) in head; caudal peduncle depth 2.8 (2.5–3.0) in head; caudal peduncle length 1.7 (1.3–1.8) in head.

Mouth large, the maxilla nearly reaching a vertical at about rear edge of pupil, the upper jaw length 1.9 (1.8–2.1) in head; mouth oblique, the gape forming an angle of 30 to 40 degrees to horizontal axis of head and body; posterior edge of maxilla concave; supramaxilla present; lower jaw slightly protruding, the tip thickened and fitting into a median indentation in upper jaw; upper jaw with a band of small villiform teeth in about 10 irregular rows on lateral portion and narrowing to 3–4 rows anteriorly; indented median part of upper jaw edentate; 3–4 irregular rows of similar teeth in lower jaw, the anterior ones recumbent; a narrow band of small villiform teeth on vomer and palatines. Tongue broad-based, gradually tapered anteriorly, the upper surface with scattered papillae.

Anterior nostril a small, low-rimmed tube, directly in front of centre of eye, about half distance from edge of orbit to front of upper lip; posterior nostril ovate without a rim, about twice size of anterior nostril, situated on a line connecting anterior nostril and top of eye. Head with

numerous, tiny lateralis system pores, but enlarged pore present at front edge of snout and on middle of preorbital. A single, flat, obtuse opercular spine. Serrations on head bones scarcely evident in small juveniles, becoming more prominent and increasing in number with added growth. Preopercular margin weakly serrate in adults (18 serrae on left side of holotype, 25–40 on paratypes); preopercular ridge mainly smooth or weakly crenulate, except for 8 (8–20) serrae; ventral and posterior portion of circumorbitals with 13 (5–13) serrae.

Scales ctenoid. Lateral line conspicuous, nearly paralleling dorsal contour of body, and ending a short distance posterior to caudal-fin base (5 pored scales posterior to hypural, the last pointed). No scales on dorsal and anal fins except a low sheath at base of second dorsal and anal fins; small scales on basal third of caudal fin; no scales on paired fins except a pair of large midventral scales at base of pelvic fins.

Origin of first dorsal fin above second lateral-line scale; first dorsal spine slender and short, 22.8 (14.3–22.0) in head; third dorsal spine longest, 2.3 (2.2–2.6) in head; second soft dorsal and anal rays longest, damaged in holotype, but their length 1.5–1.9 in paratypes; origin of anal fin below base of fourth dorsal soft ray; first anal spine short, 12.1 (10.3–18.6) in head; second anal spine 4.7 (2.8–3.5) in head; caudal fin slightly forked, its length 1.1–1.3 (damaged in holotype); origin of pelvic fins about even with pectoral-fin base; first pelvic soft ray longest, reaching beyond anus or beyond (to

anal fin origin in one paratype), its length 2.3 (1.6–2.0) in head.

Colour.

Live colours unknown, but probably similar to other members of the subgenus *Pristiapogon*, which are generally whitish with a black midlateral stripe. Colour in alcohol as follows: very pale tan with relatively narrow midlateral brown stripe from upper edge of preopercle to base of caudal fin, tapering in width posteriorly.

Remarks

This species is known only from the type specimens, but further collecting in northern Australia and adjacent seas will probably increase the distributional limits. It occurs over soft bottoms in depths as shallow as 1 m. The maximum depth limit requires additional documentation, but it apparently ranges onto the outer portion of the continental shelf.

This species belongs to the subgenus *Pristiapogon* Klunzinger as defined by Fraser and Lachner (1985). It is very similar in appearance to *A. abrogramma* Fraser and Lachner from scattered localities in the tropical Indian Ocean and western Pacific. Both species are characterized by a single dark, midlateral stripe. However, *A. unitaeniatus* has an increased number of gill rakers and pectoral rays (22–25 and 15 versus 17–19 and 13, rarely 14 respectively). The new species is named

unitaeniatus (Latin: single-striped) in reference to its characteristic colour pattern feature.

ACKNOWLEDGEMENTS

John Paxton, Douglass Hoese, Mark McGrouther, and Sally Reader provided working facilities and assistance with the fish collection and computer records during a visit to the Australian Museum in 1992. Helen Larson of the Northern Territory Museum directed my attention to the specimens of *A. unitaeniatus* in the NTM collection. Mark Cowan and Suzanne Longbottom (WAM) assisted with proportional measurements. The drawing of *Apogon unitaeniatus* was prepared by Mark Cowan.

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Manuscript received 6 May 1994; accepted 13 February 1995.

Notes on the Corixidae and Notonectidae (Hemiptera: Heteroptera) of southern Western Australia

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Abstract – The nektonic water-bugs (Corixidae and Notonectidae) collected during recent surveys in southern Western Australia are listed. *Anisops baylyi* sp. nov. is described from a number of widely distributed localities. The variation between the forms of some *Anisops* species recorded is commented on and brief notes on the extra-limital distribution of the water-bugs within Australia are given.

INTRODUCTION

The fauna of temporary pools on granite outcrops in the Northcliffe region and other widely distributed localities were sampled in 1977 (Bayly 1982). Further collections were made by Bayly during the winter of 1990 and those were in part made from habitats not on granite rock strata (Bayly 1992a). For data on rainfall pattern and physico-chemical parameters of pools on granite see Bayly (1982). Some general features of temporary pools on granite inselbergs in southern Western Australia are discussed by Bayly (1992b). Other samples collected from habitats on the Swan Coastal Plain are included as the new species *Anisops baylyi* was found by F. Cheal to occur in this region as well as in several other widely distributed localities in the Bayly samples.

The water-bug fauna of southern western Australia has some similarities with those found in south eastern Australia. The number of species in the genera recorded from both regions as compared with the total number of described Australian species are shown in Table 1.

Three endemic species were identified: *Paranisops endymion* (Kirkaldy), *Notonecta handlirschi* Kirkaldy (a specimen of this species studied from the Swan Coastal Plain leg F. Cheal) and *Sigara mullaka* Lansbury.

The data extracted from Bayly's samples tends to suggest that the water-bug fauna of southern Western Australia is depauperate compared with that of south eastern Australia. This may reflect the type of habitats sampled by Bayly and a broader range of sampling would increase the overall species diversity. Bayly sampled 49 habitats in 1977, some were sampled several times, water-bugs were found in 18. In 1990, 86 habitats sampled (two previously sampled in 1977) and

water-bugs were found in 27 samples.

The species diversity of the two series of Bayly's samples do not differ significantly allowing for the greater number of habitats sampled in 1990. A small number of *Anisops* females could not be identified and are excluded from the study.

Especially noticeable is the lack of *Sigara* species other than *S. mullaka*. Samples from Victoria and South Australia collected by the author frequently included two species, *S. truncatipala* (Hale) and *S. sublaevifrons* (Hale), occasionally three species with *S. australis* (Fieber).

There is some evidence that at least two *Anisops* species e.g., *A. thienemanni* Lundblad recorded from many habitats and *A. elstoni* Brooks recorded from several localities in southwestern Australia differ in some features (size and secondary sexual characters) from forms recorded from other regions in Australia.

The species listed or mentioned other than *N. handlirschi* are the most commonly encountered in southern Western Australia. The list only represents the species in the Bayly samples and small series from the Swan Coastal Plain, F. Cheal.

MATERIAL AND METHODS

The type series of *Anisops baylyi* from the Swan Coastal Plain will be deposited in the Western Australian Museum, Perth (WAM). Some of the Bayly material will be placed in the Museum of Victoria, Melbourne (NMV) with voucher specimens retained in Oxford (OUM). All the material is alcohol-preserved. Figures were drawn from either slide mounted preparations or from temporarily dried material which was then returned to alcohol.

SYSTEMATICS

Family Corixidae Leach

Subfamily Diaprepocorinae Lundblad

Diaprepocoris personata Hale

Diaprepocoris personata Hale, 1924: 7–10; Knowles, 1974: 187–189.

Material Examined

Australia: Western Australia: 1 ♂, roadside pool 6.7 km S. of Northcliffe [locality 4 of Bayly (1992a)], 18 June 1977; 1 ♀, 1 July 1977. 1 ♂, 1 ♀, pool on Muirillup Rock [locality 4 of Bayly (1982)] 34°39'S, 116°15'E, 2 July 1990.

Remarks

Described by Hale (1924) from Western Australia (Swan River). Knowles (1974) localities are all in Western Australia. I have seen material from Tasmania, South Australia (Mt Gambier region) and Queensland (Brisbane).

Subfamily Corixinae Leach

Sigara mullaka Lansbury

Sigara mullaka Lansbury, 1970: 42–44

Material Examined

Australia: Western Australia: 1 ♂, 3 ♀, granite rock pools on Sullivan Rock, 11 km S. of Gleneagle [locality 10 of Bayly (1982)], 8 June 1977. 1 ♀, granite rock pool, Bunjil Rocks, 24 km S. of Perenjori, 29°39'S, 116°21'E, 13 July 1990. 1 ♂, 1 ♀, pool on Sanford Rocks, 31°14'S, 118°46'E, 15 August 1990.

Remarks

Previously recorded from Western Australia (Mt Yokine, Bickley Swamp, Darling Ranges and Newcastle).

Table 1 Numbers of species of Notonectidae and Corixidae in Australia.

	Southeastern Australia	Southwestern Australia	Australian total
Notonectidae			
<i>Anisops</i>	10	6	27
<i>Paranisops</i>	1	1*	2
<i>Enithares</i>	2	0	4
<i>Notonecta</i>	0	1*	1
Corixidae			
<i>Diaprepocoris</i>	3	2	3
<i>Sigara</i>	6	1*	7
<i>Agraptocorixa</i>	3	3	6
<i>Micronecta</i> **	?	3	14?

* endemic to S.W. Australia

** taxonomy of *Micronecta* confused, in need of revision.

Agraptocorixa parvipunctata (Hale)

Agraptocorixa parvipunctata (Hale), 1922: 320–321; Lundblad, 1928: 13–18; Knowles, 1974: 177–179.

Material Examined

Australia: Western Australia: 1 ♂, roadside pool 7.1 km S. of Northcliffe [locality 5 of Bayly (1992a)], 2 July 1977; 2 ♂, 2 ♀, Newmann's Rocks, 88 miles E. of Norseman [locality 18 of Bayly (1982)], 5 July 1977; 1 ♂, granite rock pool, summit Mt Madden, N. of Ravensthorpe, 33°14'S, 119°50'E, 26 June 1990; 1 ♀, rock pool about 2 m below main summit pool, Mt Madden, 33°14'S, 119°50'E, 26 June 1990; 1 ♀, roadside pool 15 km W. of Denmark, 34°59'S, 117°10'E, 29 June 1990; 1 ♂, 1 ♀, Rock pool, War Rock, Pitharuka Dam Road, ca. 15 km N Morawa, 29°05'S, 116°00'E, 13 July 1990. 16 ♂, 22 ♀, granite rock pool, Bunjil Rocks, 24 km S. of Perenjori, 29°39'S, 116°21'E, 13 July 1990; 18 ♂, 41 ♀, granite rock pool, Petrudor Rock, 30°25'S, 116°58'E, 14 August 1990.

Remarks

Described from South Australia (Adelaide). Widespread over much of Australia. Found as far north as Julatten north of Cairns, Queensland.

Agraptocorixa eurynome (Kirkaldy)

Agraptocorixa eurynome (Kirkaldy), 1897: 54–55; Hale, 1922: 318–319; Lundblad, 1928: 3–9; Knowles, 1974: 175–177; Jansson, 1982: 88.

Material Examined

Australia: Western Australia: 7 ♂, roadside pool 3.1 km S. of Warren River near Manjimp, 28 May 1977; 4 ♂, 1 ♀, roadside pond 2.3 km S. of Northcliffe [locality 2 of Bayly (1992a)], 3 June 1977; 1 ♂, 1 ♀, roadside pond 10.8 km S. of Northcliffe [locality 6 of Bayly (1992a)], 3 June 1977. 3 ♂, 1 ♀, small permanent lake behind Hamelin Bay, NW. of Augusta, 34°13'S, 115°02'E, 5 July 1990.

Remarks

Males varying between 7.6–8.13 mm long, females 8.3 mm long, smaller than usual, Knowles (1974) gives length as 8.5–10 mm long.

Kirkaldy (1897) described *eurynome* from the 'Adelaide River' South Australia. Hale (1922) and Knowles (1974) place the type locality in the Northern Territory. The most northerly Australian records published are the Hann River and Townsville, Queensland, (Knowles litt. comm.). Extensive collections from the Northern Territory have shown that *eurynome* does not occur much further north than Alice Springs. The commonest species in the 'far north' is *Agraptocorixa halei* Hungerford (Northern Territory Museum collections).

Jansson (1982) however, has recorded *eurynome* from Irian Jaya: New Guinea (NW) Wisselmeren, Itouda, Kamo, 1500 m. which supports the possibility that *eurynome* occurs in the far north of Australia.

Subfamily Micronectinae Jaczewski

Remarks

The taxonomy of the Australian *Micronecta* is in need of revision. Some of the Bayly samples included two or possibly three species. Males were selected of each species, measured and dissected, they were found to differ in minor details from those figures by Wroblewski (1970). Females in the samples seemed to lack obvious distinguishing features other than size. No attempt was made to give numbers of both sexes in samples owing to the possibility of taxonomic error.

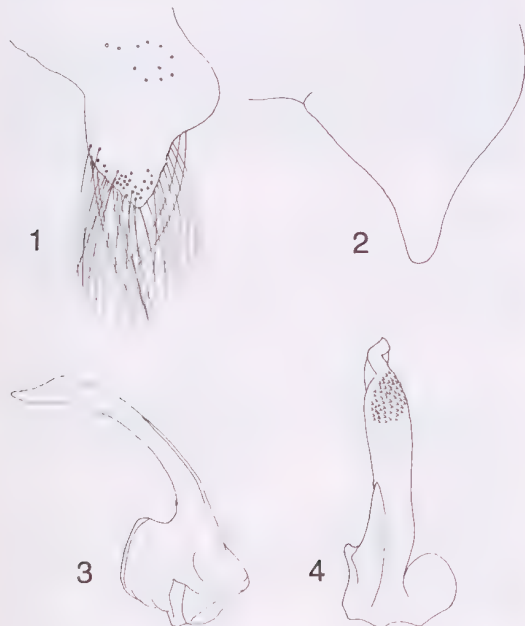
Micronecta robusta Hale

Figures 1–4

Micronecta robusta Hale, 1922: 325; Chen, 1965: 153–155; Wroblewski, 1970: 689–691; 1977: 687–688.

Material Examined

Australia: Western Australia: rock pools near summit Mt Madden, 33°14'S, 119°50'E, 26 June



Figures 1–4 *Micronecta robusta* Hale, ♂, Bunjil Rocks: 1, free lobe of 8th tergite; 2, process of 7th sternite; 3, right paramere; 4, left paramere. Scale line 0.5 mm.

1990; granite rock pool, Bunjil Rocks, 24 km S Perenjori, 29°39'S, 116°21'E, 13 July 1990 (males 3.68 mm long, 1.8 mm wide); pool, SW. corner of Elachbutting Rock, 30°36'S, 118°37'E, 15 August 1990 (males 3.68–3.76 mm long, 1.84 wide); pool on Sanford Rocks, 31°14'S, 118°46'E, 15 August 1990 (males 3.72 mm long, females 4 mm long); pool near summit of Wave Rock, E. of Hyden, 32°27'S, 118°54'E, 28 August 1990 (female 4.24 mm long, 1.92 mm wide).

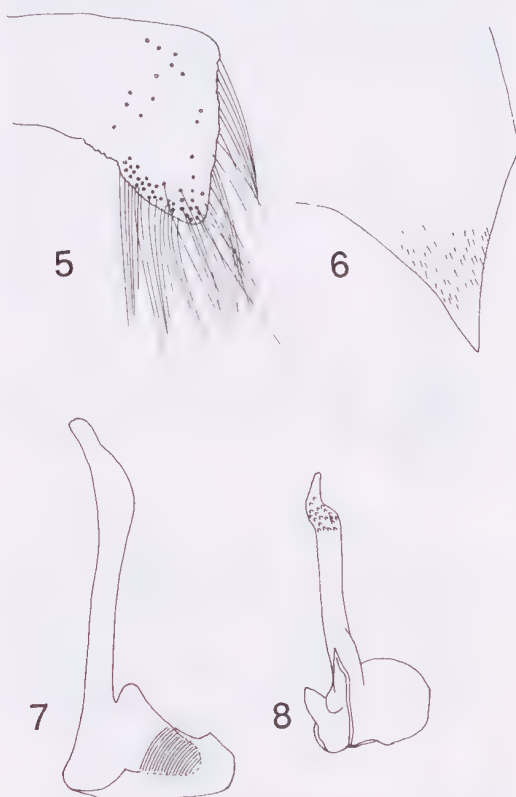
Remarks

Figures 1–4 show details of the male genitalia. Type locality South Australia: Adelaide. Widely distributed in southeastern Australia, Tasmania and Western Australia, see Wroblewski (1970, 1977).

Micronecta gracilis Hale

Figures 5–8

Micronecta gracilis Hale, 1922: 326; Chen, 1965: 151–155; Wroblewski, 1970: 692–694; 1977: 688.



Figures 5–8 *Micronecta gracilis* Hale, ♂, Bunjil Rocks: 5, free lobe of 8th tergite; 6, process of 7th sternite; 7, right paramere; 8, left paramere. Scale line 0.5 mm.

Material Examined

Australia: Western Australia: long series of both sexes, granite rock pool, Bunjil Rocks, 24 km S. of Perenjori, 29°39'S, 116°21'E, 13 July 1990 (3.4 mm long, 1.4 mm wide); series of both sexes, pool on Petrudor Rocks, 30°25'S, 116°58'E, 14 August 1990 (3.32–3.56 mm long, 1.44–1.52 mm wide).

Remarks

Figures 5–8 show details of the male genitalia. Type locality South Australia: Quorn. Widely distributed in Victoria, New South Wales and southern Queensland.

***Micronecta annae* Kirkaldy**

Figures 9–12

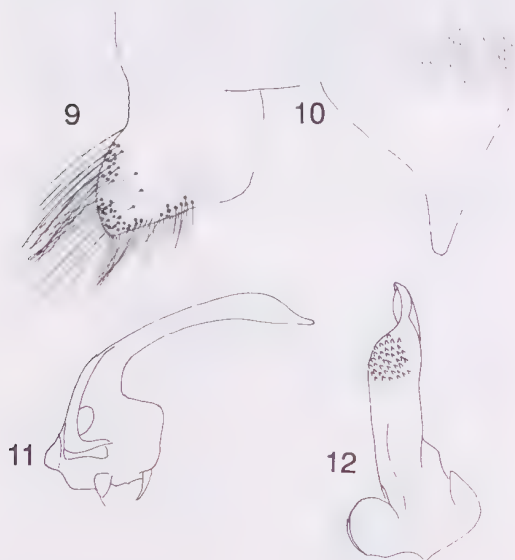
Micronecta annae Kirkaldy, 1905: 262–263; Chen, 1965:162; Wroblewski, 1970: 682–687; 1977: 684.

Material Examined

Australia: Western Australia: rock hole, War Rock, Pitharuka Dam Road ca. 15 km N. of Morawa, 29°05'S, 116°00'E, 13 July 1990 (females 3.56–3.68 mm long, 2.2–2.3 mm wide); deep pool on Beringbooding Rock, 30°34'S, 118°30'E, 15 August 1990 (females 3.4–3.52 mm long, 1.52–1.64 mm wide).

Remarks

Figures 9–12 show details of the male genitalia.



Figures 9–12 *Micronecta annae* Kirkaldy, ♂, Beringbooding Rock: 9, free lobe of 8th tergite; 10, process of 7th sternite; 11, right paramere; 12, left paramere. Scale line 0.5 mm.

Type locality Victoria, no precise locality. Widely distributed in Australia (Wroblewski 1970, 1977).

Family Notonectidae Latreille**Subfamily Anisopinae Hutchinson*****Paranisops endymion* (Kirkaldy)**

Anisops endymion Kirkaldy, 1904: 112; Brooks, 1951: 463–464 (references 1904–1933).

Paranisops endymion (Kirkaldy): Lansbury, 1964b: 181–188.

Material Examined

Australia: Western Australia: 2 ♂, 3 ♀, swamp 800 m from Le Grand Beach camping ground, Cape le Grand National Park, 33°58'S, 122°07'E, 25 June 1990.

Remarks

Also recorded from Lake Gnangara, Swan Coastal Plain (Lansbury 1964b).

Type locality, Western Australia: Swan River.

***Anisops stali* Kirkaldy**

Anisops stali Kirkaldy, 1904: 113, 132; Brooks, 1951: 319–322 (references 1904–1934); Sweeney, 1965: 90; Lansbury, 1969: 434–437.

Material Examined

Australia: Western Australia: 1 ♂, pit-gnamma beside War Rock, Pitharuka Dam road, N. of Morawa, 29°05'S, 116°00'E, 13 July 1990; 6 ♂, 6 ♀, pool on Petrudor rocks, 30°25'S, 116°58'E, 14 August 1990.

Remarks

Described from 'Australia'. Species widespread over most of Australia other than Tasmania. Recorded from much of Indonesia, New Hebrides, Philippines northwards to Okinawa.

***Anisops deanei* Brooks**

Anisops deanei Brooks, 1951: 381–382; Sweeney, 1965: 90; Lansbury, 1964a: 62–64; 1969: 434, 455, 457.

Material Examined

Australia: Western Australia: 1 ♂, roadside pool at Windy Harbour, 27 km S. of Northcliffe, 1 July 1990.

Remarks

Type series from New South Wales: Bogan River, Victoria: Alexandria and Queensland: St George District. Widespread over much of 'southern' Australia northwards to Alice Springs.

Anisops gratus Hale

Anisops gratus Hale, 1923: 413–414; Brooks, 1951: 352–353; Sweeney, 1965: 91; Lansbury, 1969: 448–449.

Material Examined

Australia: Western Australia: 2 ♀ and immatures, Lake Cronin, 85 km E. of Hyden, 32°23'S, 119°45'E, 28 August 1990; 1 ♀, pool on Petrudor Rocks, 30°25'S, 116°58'E, 14 August 1990.

Remarks

Type series from New South Wales: Broken Hill; Hale (1923) also included localities in South Australia, Northern Territory, Queensland and Western Australia. The most northerly record so far known is from the Elkedra River ca. 340 km NE. of Alice Springs.

Anisops thienemanni Lundblad

Figures 13–14

Anisops thienemanni Lundblad, 1933: 167–168; Brooks, 1951: 413–416; Sweeney, 1965: 88–89; Lansbury, 1969: 446–448.

Material Examined

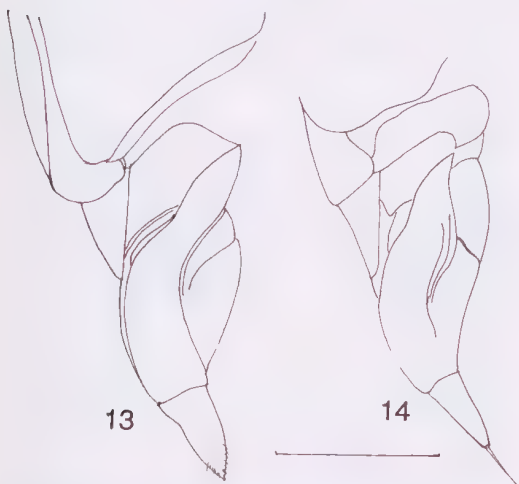
Australia: Western Australia: 6 ♂, 11 ♀, roadside pool, Pfeiffer's Road, 8 km from Many Peaks, 4 July 1977; 1 ♂, 1 ♀, roadside pool, 3 km S. of Warren River, near Manjimup, 28 May 1977; 2 ♂, 2 ♀, roadside pool, 2.3 km S. of Northcliffe [locality 1 of Bayly (1992a)], 1 July 1977; 4 ♀, roadside pool 6 km S Northcliffe [locality 3 of Bayly (1992a)], 18 June 1977; 4 ♀, roadside pool, 6.7 km S. of Northcliffe [locality 4 of Bayly (1992a)], 18 June

1977; 3 ♀, roadside pool, 7.1 km S. of Northcliffe [locality 5 of Bayly (1992a)], 17 June 1977; 1 ♀, 2 July 1977; 1 ♂, 2 ♀, granite rockpool on Muirillup Rock near Northcliffe [locality 4 of Bayly (1982)], 18 June 1977; 2 ♂, 3 ♀, granite rock pools on Sullivan Rock, 11 km S. of Gleneagle [locality 10 of Bayly (1982)], 8 June 1977; 1 ♀, large shallow pad-dock pond, South Harvey Estuary, 5.5 km along Warooma Road from coast road, 1 July 1977; 1 ♀, small shallow lake near eastern side of Lake Powell, 3 July 1977; 1 ♀, ponds near Frenchman's Bay Road, Albany, 3 July 1977; 3 ♀ [6.8–7.47 mm long], three inter-connecting pools on summit of Mt Madden, N. of Ravensthorpe, 33°14'S, 119°50'E, 26 June 1990; 1 ♂ [7.55 mm long], rock pool about 2 m below summit pool, Mt Madden, 33°14'S, 119°50'E, 26 June 1990; 1 ♀ [8.46 mm long, doubtfully *thienemanni*], roadside pool 15 km W. of Denmark, 34°59'S, 117°10'E, 29 June 1990; immatures, roadside pool near Northcliffe [locality 2 of Bayly (1992a)], 1 July 1990 [possibly *thienemanni*]; 1 ♀, [7.13 mm long], roadside pool near Northcliffe [locality 3 of Bayly (1992a)]; 2 ♀ [7.47 mm long], roadside pool near Northcliffe [locality 4 of Bayly (1992a)]; 3 ♂ [6.7–7.8 mm long] 5 ♀, immatures [6.8–7.7 mm long], rock-pool on War Rock, Pitharuka Dam Road, ca. 15 km N. of Morawa, 29°05'S, 116°00'E, 13 July 1990 (Fig. 13); 1 ♂, [7.63 mm long], pit-gnamma beside War Rock, Pitharuka Dam Road, N. of Morawa 29°05'S, 116°00'E, 13 July 1990; 5 ♂, 12 ♀ [7.47 mm long], section of granite rock artificially dammed at Bunjil Rocks, 24 km S. of Perenjori, 29°39'S, 116°21'E, 13 July 1990; 1 ♀, pool on Petrudor Rocks, ca. 20 m lower than summit, 30°25'S, 116°58'E, 14 August 1990; 3 ♂, 3 ♀, pool on Petrudor Rocks, 30°25'S, 116°58'E, 14 August 1990; 5 ♂ [7.1–7.47 mm long], 6 ♀ [7.0–7.38 mm long], deep pool on Beringbooding Rock, 30°34'S, 118°30'E, 15 August 1990; 2 ♀ [7.3 mm long], pool on SW. corner of Elachbutting Rock, 30°36'S, 118°37'E, 15 August 1990.

Remarks

Type series, Java, Mitteljava, Diengplateau, See Telaga Warnaetwa 2000 masl; Diengplateau, Chara-Tümpel gegenüber der Kawa Sikidang. Found over most of 'southern' Australia, distribution similar to *A. gratus*. Some of the samples from southern Western Australia are consistently larger than material from other regions of Australia. Brooks (1951) states males 6–7.2 mm long, females 6–6.9 mm long; Lansbury (1969) males 6.9–7.2 mm long, females 6.75–7.5 mm long; southwestern Australia series, males 6.7–7.8 mm long, females 6.8–7.7 mm long. Javanese type 7.5 mm long.

In Australia, *A. thienemanni* has not been found much further north than the Elkedra River, ca. 340 km NE of Alice Springs. The rostral prong of male



Figures 13–14 *Anisops thienemanni* Lundblad, ♂: 13, rostral prong, War Rock; 14, rostral prong, N.T. Elkedra. Scale line 0.5 mm.

from South Western Australia (Fig. 13) differs from the Northern Territory form (Fig. 14) and both are distinct from the form figured from S.E. Australia by Lansbury (1969: 447, fig. 46).

It is possible that *thienemanni* may be a group of sibling species. The distribution gap between its widespread occurrence over 'southern' Australia including Tasmania and the apparently sparse records from Java does need further investigation.

Anisops baylii sp. nov.

Figures 15–17

Material Examined

Holotype

♂, Lake Mt Brown, Swan Coastal Plain, Perth, Western Australia, Australia, 10 December 1993, F. Cheal (WAM 95/498).

Paratypes

Australia: Western Australia: 1 ♂, 9 ♀, same collection data as holotype; 7 ♂, same data as holotype, November–December 1992; 1 ♂, Lake Nowergup, Swan Coastal Plain, Perth, 10 February 1989, F. Cheal; 3 ♂, 1 ♀, Brownman Swamp, Swan Coastal Plain, Perth, 3 November 1989, F. Cheal (WAM); 6 ♂, Lake Mt Brown, Summer 1992, F.

Cheal (OUM); 1 ♂, 1 ♀, natural rock pools, near summit of Mt Madden, 33°14'S, 119°50'E, 26 June 1990, I.A.E. Bayly (NMV).

Other Material

Australia: Western Australia: 5 ♀, rock-pool on War Rock, Pitharuka Dam Road, ca. 15 km N. of Morawa, 29°05'S, 116°00'E, 13 July 1990, I.A.E. Bayly; 9 ♀, section of granite rock artificially dammed, Bunjil Rocks, 24 km S. of Perenjori, 29°39'S, 116°21'E, 13 July 1990, I.A.E. Bayly (OUM and NMV).

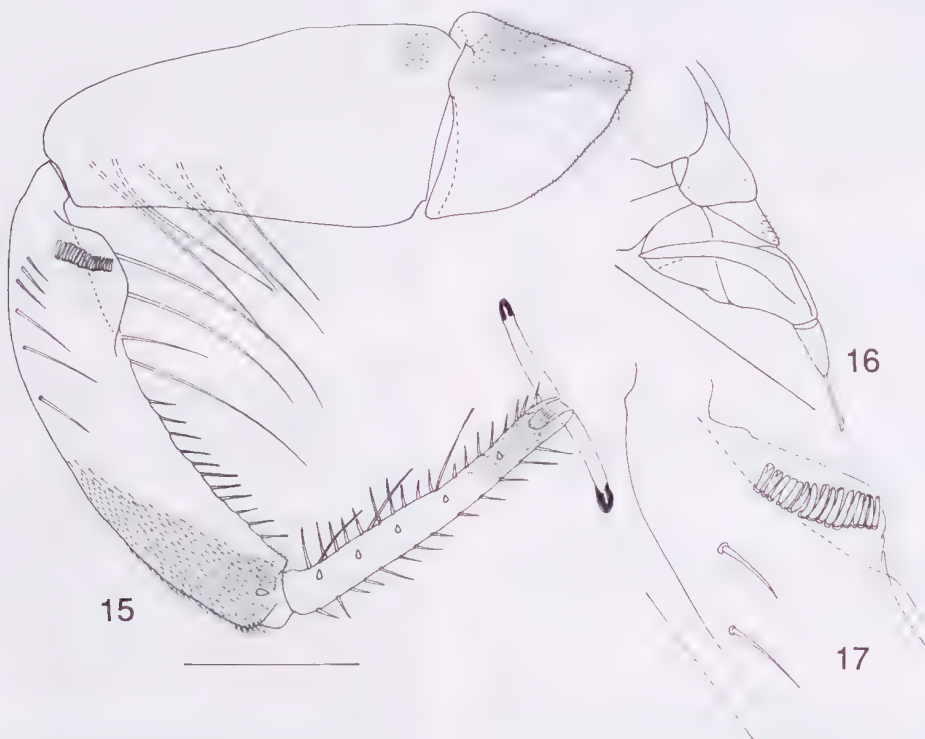
Description

Male

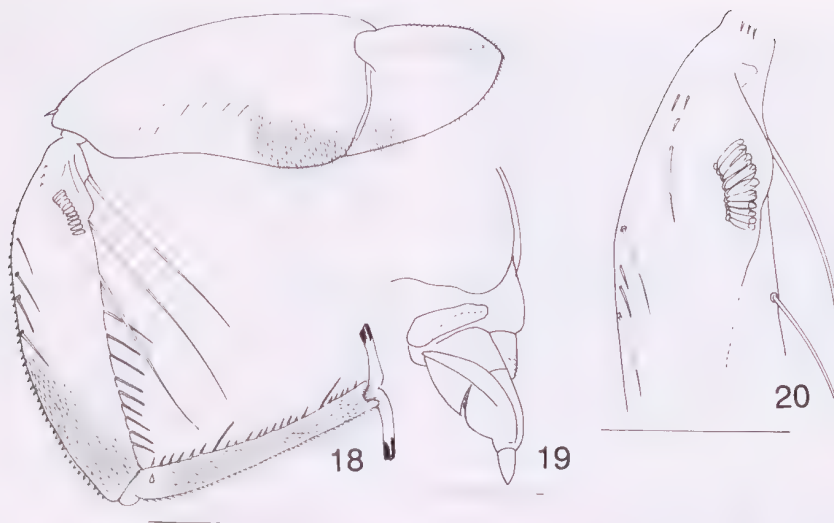
7.2–7.8 mm long; head width 1.8–1.98 mm; pronotal width 1.76–1.96 mm.

Colour: eyes black shining. Dorsal coloration varying between uniformly pale greyish yellow or with anterior lateral margins of vertex yellowish brown, remainder hyaline. Scutellum shining brown-black, apex hyaline. Hemelytra hyaline, black dorsal pigmentation showing through, laterally narrowly iridescent. Ventrally black, legs pale yellow, middle femora infuscated dark brown-black.

Structure: viewed dorsally head large, eyes large



Figures 15–17 *Anisops baylii* sp. nov., paratype ♂, Mt Madden: 15, front leg (scale line 0.5 mm); 16, rostral prong (scale line 1 mm); 17, stridulatory comb (scale line 0.25 mm).



Figures 18–20 *Anisops elstoni* Brooks, ♂, Cape Le Grand National Park: 18, front leg (scale line 0.5 mm); 19, rostral prong (scale line 0.5 mm); 20, stridulatory comb (scale line 0.25 mm).

extending slightly in front of the anterior width of vertex. Greatest head width either as wide or wider than greatest width of pronotum. Maximum head width between 7.5–9.8x anterior width of vertex and 3x median head length. Synthlipsis wide varying between 0.6–0.9x anterior width of vertex. Median head length 0.6–0.7x median pronotal length. Pronotal width 2x median length, lateral margins almost straight and slightly divergent. Posterior margin medianly slightly emarginate. Facial tubercle slightly raised with short sparse greyish hairs. Rostral prong long and thin (Figure 16). Basal width of labrum subequal to median length with longer hairs. Stridulatory comb (Figure 17) 15 pegs, inner pegs appearing distally acuminate. Chaetotaxy of front leg (Figure 15).

Female

7.0–7.8 mm long; head width 1.68–1.84 mm; pronotal width 1.82–1.92 mm.

Colour: similar to male.

Structure: viewed dorsally lateral eye margins convergent. Greatest head width between 0.89–0.93x pronotal humeral width and between 2.8–3.2x anterior width of vertex. Head width between 5.3–8.3x anterior width of vertex. Synthlipsis between 0.62–0.92x anterior width of vertex. Median pronotal length 1.3–1.7x median head length, pronotal humeral width 1.89–2.25x median length. Lateral pronotal margins straight, diverging, posterior margin medianly emarginate. Facial tubercle slightly raised, frons above facial tubercle with fine pale hairs. Labrum with a cluster of short fine hairs. Basal width of labrum subequal to median length.

Remarks

In Brooks (1951) this species keys out to *leucothea* Esaki and in Lansbury (1969) it keys out to *occipitalis* Breddin. The stridulatory comb of *occipitalis* has about 24–26 pegs and the dorsal margin of the front femur is sinuate distally whereas that of *baylii* is more or less straight. The rostral prong of both *leucothea* and *occipitalis* are wider basally than *baylii* which has a very narrow elongate rostral prong.

Anisops elstoni Brooks

Figures 18–20

Anisops elstoni Brooks, 1951: 326–327; Lansbury, 1964a: 58–59; Sweeney, 1965: 91; Lansbury, 1978: 105–107.

Material Examined

Australia: Western Australia: 2 ♂, roadside pool, Pfeiffer's Road, 8 km from Many Peaks, 4 July 1977; 2 ♂, roadside pool, 6 km S. of Northcliffe [locality 3 of Bayly (1992a)], 1977; 1 ♂, 1 ♀, swamp 800 m from Le Grand Beach camping ground, Cape Le Grand National Park, 33°58'S, 122°07'E, 25 June 1990.

Description

Males and females 5.8 mm long.

Colour: eyes dark brown. Pronotum and scutellum pale brownish yellow. Hemelytra hyaline, dorsal pigmentation showing through. Ventrally black including frons, facial tubercle and labrum. legs shining dark brown-black.

Male

Viewed dorsally eyes large, lateral margins slightly convex. Greatest head width fractionally narrower than pronotal humeral width, $6.8\times$ anterior width of vertex and almost $3\times$ median head length. Synthlipsis $0.4\times$ anterior width of vertex. Median head length $0.8\times$ median pronotal length. Pronotal width $2.12\times$ median length, lateral margins diverging, posterior margin laterally deeply concave, medianly deeply emarginate. Facial tubercle slightly raised. Median labral length equal to basal width, distally broadly rounded with sparse fine hairs. Chaetotaxy of front leg (Figure 18) tarsus with a prominent proximal spine. Stridulatory comb small with *ca.* 13 even-sized pegs (Figure 20). Rostral prong (Figure 19).

Females

Greatest head width narrower than pronotum and $5.75\times$ anterior width of vertex and $3\times$ median head length. Synthlipsis $0.4\times$ anterior width of vertex. Median head length $0.67\times$ median pronotal length. pronotal width $2.2\times$ median length, lateral margins strongly divergent, posterior margin similar to male.

Remarks

Brooks (1951) described *elstoni* from various localities in Australia and China, Suifu, Szechwan. *Anisops depressa* Lansbury from Irian Jaya appears to be a synonym of *elstoni* (Lansbury 1978). The form from southwestern Australia differs from the 'typical form' by its larger size, 5.8: 4.5–5.0 mm, absence of the depressions on the male pronotum and the slightly larger more robust rostral prong.

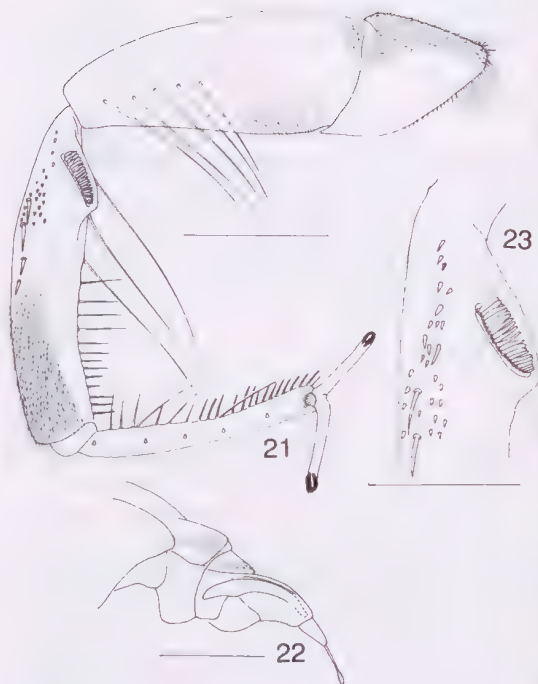
***Anisops hyperion* Kirkaldy**

Figures 21–23

Anisops hyperion Kirkaldy, 1898: 141; Brooks, 1951: 332–334 (references 1898–1951); Sweeney, 1965: 89–90; Lansbury, 1964a: 61–62; Lansbury, 1969: 434, 456–457.

Material Examined

Australia: Western Australia: 7 ♂, 4 ♀, roadside pool, 3 km S. of Warren River, Manjimup, 28 May 1977; 9 ♂, 1 ♀, roadside pool, 2.3 km S. of Northcliffe [locality 2 of Bayly (1992a)], 3 June 1977; 1 ♂, 1 ♀, roadside pool, 6 km S. of Northcliffe [locality 3 of Bayly (1992a)], 18 June 1977; 1 ♂, 1 ♀, granite rock pool at top of Mt Madden, 4 July 1977; 1 ♂, artificial pond at base of Ponier Rock, $32^{\circ}56'E$ $123^{\circ}30'E$, 24 June 1990; 1 ♂, roadside pond, Cape le Grand National Park, $33^{\circ}56'S$, $122^{\circ}11'E$, 25 June 1990; 3 ♀, large pool, summit of Mt Madden,



Figures 21–23 *Anisops hyperion* Kirkaldy, ♂, Mt Madden: 21, front leg; 22, rostral prong (scale lines 0.5 mm); 23, stridulatory comb (scale line 0.25 mm).

N. of Ravensthorpe, $33^{\circ}14'S$, $119^{\circ}50'E$, 26 June 1990; 1 ♂, 1 ♀, rock-pool, *ca.* 20 m below summit pool, Mt Madden, $33^{\circ}14'S$, $119^{\circ}50'E$, 26 June 1990; 1 ♂, roadside pool, 15 km W. of Denmark, $34^{\circ}59'S$, $117^{\circ}10'E$, 29 June 1990; 1 ♂, roadside pool near Northcliffe [locality 4 of Bayly (1992a)], 1 July 1990; 3 ♂, pit-gnamma beside War Rock, Pitharuka Dam Road, N. of Morawa, $29^{\circ}05'S$, $116^{\circ}00'E$, 13 July 1990; 3 ♂, 1 ♀, section of granite rock artificially dammed, Bunjil Rocks, 24 km S. of Perenjori, $29^{\circ}39'S$, $116^{\circ}21'E$, 13 July 1990; 8 ♂, 8 ♀, pool on Petrudor Rocks 20 m below summit, $30^{\circ}25'S$, $116^{\circ}56'E$, 14 August 1990; 1 ♂, 1 ♀, deep pool on Beringbooding Rock, $30^{\circ}34'S$, $118^{\circ}30'E$, 15 August 1990.

Description*Male*

Composite description based on males from four South Western Australian localities, form variable.

6.14–6.8 mm long.

Greatest head width between 0.89 – $0.91\times$ pronotal humeral width, 7 – $7.8\times$ anterior width of vertex and 2.1 – $2.57\times$ median head length. Synthlipsis 0.38 – $0.42\times$ anterior width of vertex. Median head length 0.87 –subequal to median pronotal length. Pronotal

humeral width 2.2–2.3x median length. Lateral margins straight, diverging, posterior margin medianly emarginate. Facial tubercle very slightly raised. Labrum, basal width subequal–1.3x median length. Both facial tubercle and labrum with scattered short semi-erect hairs. Chaetotaxy of front leg (Figure 21). Rostral prong (Figure 22). Stridulatory comb (Figure 23) with 19 pegs.

Remarks

In Brooks (1951) the form from South Western Australia keys out to *deanei* Brooks. *A. hyperion* is easily distinguished by the apex of the 3rd rostral segment not being wider than the base of the 4th as it is in *deanei*.

ACKNOWLEDGEMENTS

I wish to thank Dr I.A.E. Bayly (Monash University) for sending me his collections from South Western Australia and for his very helpful comments on the first draft of the manuscript. Finally to Dr Faye Cheal (Murdoch University) for sending me various samples from the Perth area and permitting me to include some of her data in this account.

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Manuscript received 6 April 1994; accepted 31 January 1995.

The *Myotis adversus* (Chiroptera: Vespertilionidae) species complex in Eastern Indonesia, Australia, Papua New Guinea and the Solomon Islands

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Abstract – Comparison of cranial, external and bacular morphology and univariate and multivariate statistical analyses of 149 specimens, previously attributed to *Myotis adversus* (Horsfield, 1824) was carried out on specimens principally from eastern Indonesia and Australia. These comparisons indicated the existence of a complex of three species and six subspecies. These taxa are as follows: *Myotis a. adversus* (Java I., Nusa Penida I., Kangean I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Timor I., Savu I.); *Myotis adversus tanimbarensis* subsp. nov. (Yamdena I.); *Myotis adversus wetarensis* subsp. nov. (Wetar I.); *Myotis moluccarum moluccarum* (Western Australia, Seram and Papua New Guinea; and possibly also including the form from Solomon I.); *Myotis moluccarum richardsi* subsp. nov. (Queensland, Northern Territory) and *Myotis macropus* (Victoria and South Australia).

These above taxa have not previously been reported from Nusa Penida I., Kangean I., Sumbawa I., Moyo I., Lembata I., Pantar I., Alor I., Savu I., Yamdena I., and Wetar I.

Multiple regression analysis indicated that while the skull, dentary and dental characters of the above *Myotis* were not significantly influenced by sex, many of the wing measurements were influenced by sex. Almost all characters were very significantly ($P < 0.001$) influenced by locality, but there was no significant interaction between sex and locality.

INTRODUCTION

Myotis adversus (Horsfield, 1824) is a medium sized member of the subgenus *Leuconoe* Boie, 1830 that is characterised by unusually large feet. The species has a wide distributional range from Taiwan, Malaysia, Greater Sunda Islands (Sumatra, Java and Borneo), Lesser Sunda Islands (Flores), Karimata Island, Togian Islands, Peleng Island; Talaud Islands, Maluku Region (Seram, Ambon, Kai Islands), Solomon Islands, New Hebrides and Australia. Over its range it is morphologically very variable; some of this variation has been recognised taxonomically.

A number of authors have reviewed or commented upon the taxonomy of *Myotis adversus* (Tate 1941; Phillips and Birney 1968; Medway 1977; Findlay 1972; Hill 1983; Hill in Corbet and Hill 1992). The subspecies of *M. adversus* generally recognised are:

Myotis adversus adversus (Horsfield, 1824) – Java, Lesser Sunda Islands, Malaysia (?);

M. a. taiwanensis Arnback-Christie Linde, 1908 – Taiwan;

M. a. carinatae Miller, 1906 – Borneo, Karimata Island;

M. a. moluccarum (Thomas, 1915) – Sulawesi, Maluku Region, New Guinea;

M. a. solomonis (Troughton, 1929) – Solomon Islands;

M. a. orientis Hill, 1983 – New Hebrides; and

M. a. macropus (Gould, 1855) – South Australia

Hill (1983) followed Phillips and Birney (1968) in placing *M. a. solomonis* in synonymy with *M. a. moluccarum*.

There is some contention as to the subspecific status of the Australian form of *Myotis adversus*. Dobson (1878) compared the types of *Vespertilio macropus* with *Vespertilio adversus* and concluded that he was “quite unable to discover any difference. Both agree in dentition, in the form of the head and ears, and in all other respects”. Thomas (1915) agreed with Dobson (1878) that the type of *V. macropus* cannot be distinguished from Javanese *V. adversus*. However, Thomas (1915) incorrectly stated that the type of *V. macropus* was from Western Australia, when it was in fact from South Australia (Mahoney and Walton 1988).

Thomas (1915) included a specimen from Port Essington, Northern Territory, Australia, in his description of *Leuconoe moluccarum* and noted that



Figure 1 Locality of *Myotis* specimens examined in this study.

this form is very decidedly smaller than *M. adversus macropus* (from South Australia). Tate (1952) examined three specimens of *Myotis* (*Leuconoe*) from Cairns, Northern Queensland, Australia, and although they were of similar size to *Myotis adversus moluccarum* from New Guinea, he considered them representative of *M. adversus macropus*, rather than *M. a. moluccarum*.

Koopman (1984:12) also considered that only one subspecies of *Myotis adversus* (*macropus*) occurred in Australia and stated that its distribution extended from "northeastern Western Australia around the northern and eastern coasts to southeastern South Australia but apparently nowhere extending far inland" Richards (1983) and Mahoney and Walton (1988) recognised *M. a. moluccarum* from Northern Australia and *M. a. macropus* from south and eastern Australia.

A number of terrestrial vertebrate faunal surveys in Nusa Tenggara and the Maluku Tenggara regions of Indonesia, between November 1987 and November 1993, were carried out jointly by staff of the Western Australian Museum and Museum Zoologicum Bogoriense. These surveys resulted in extensive collections of *Myotis adversus* (*sensu lato*) on islands from which they had not previously

been recorded. These recent collections bridge the previous distributional gap between the Oriental and Australian *M. adversus* (*sensu lato*) and allow for a reappraisal of the taxonomy of some of the forms of *M. adversus*.

This paper reports on a taxonomic reappraisal of *Myotis adversus* (*sensu lato*), based on a morphological examination of specimens principally from eastern Indonesia and Australia.

MATERIALS AND METHODS

A total of 149 specimens (listed in the specimens examined section) was examined from a number of localities in the Indonesian and Australo-papuan region (Figure 1). These were from Java (2), Nusa Penida (6), Kangean Island (1), Sumbawa Island (5), Moyo Island (1), Flores Island (3), Lembata Island (1), Pantar Island (1), Alor Island (38), Wetar Island (18), Yamdena Island (8), Seram Island (1), Timor Island (1), Savu Island (4), Papua New Guinea (2), Solomon Islands (2), Queensland (12), Northern Territory (2), Western Australia (22), New South Wales (1), Victoria (14) and South Australia (4). All the specimens from Indonesia are currently lodged in the Western Australian

Museum (WAM prefix). At the completion of the project holotypes of new taxa and half the other specimens will be returned to Museum Zoologicum Bogoriense. Other specimens were borrowed from the British Museum, Natural History (BMNH), Queensland Museum (JM), Australian Museum, Sydney (AM), Museum of Victoria (C) and South Australian Museum (SAM).

Twenty measurements of skull, dentary and dental characters and 14 external characters (all in mm) were recorded to 0.1 mm for external characters and 0.01 mm for the other characters.

The measurements recorded were: GSL, greater skull length; CBL, condylobasal length; BB, braincase breadth, ZW, zygomatic width; MW, mastoid width; CH, cranial height; RL, rostrum length; AOW, width between anteorbital foramen; LIB, least interorbital breadth; PPL, postpalatal breadth; MFB, mesopterygoid fossa breadth; BUL, bulla length (excluding cochlear process); C'C'W, width between outer surface of upper canines (at level of alveoli); M³M³W, width between outer surface of upper last molars (at level of alveoli); I¹M³L, length between anterior edge of I¹ alveoli to posterior edge of M³ alveoli; C¹M³L, length between anterior edge of C¹ alveoli to posterior edge of M³ alveoli. M²B, M² crown breadth; DL, dentary length from condyle to I₁ anterior alveoli edge, I₁M₃L, length between anterior I₁ alveoli edge to posterior M₃ alveoli edge; SVL, tip of rhinarium to anus length; TV, distal tip of tail to anus length; EL, ear length; TIB, tibia length; PES, pes length; FA, forearm length; D3M, D4M and D5M – digit 3 to 5 metacarpal length; D3P1, D4P1, D5P1 – digit 3 to 5 phalanx 1 length; D3P2, D4P2 – digit 3 and digit 4 phalanx 2 length.

Pelage descriptions follow the colour terminology of Smithe (1975).

Adults were diagnosed as those specimens with all cranial sutures fused and without swelling on the epiphyseal joints of the wing digits.

The effect of sex and island on all characters, except zygomatic width (values missing from many specimens) was examined by multiple regressions for those localities with both sexes present (Java, Nusa Penida, Sumbawa, Alor, Wetar, Yamdena, Savu Western Australia, Queensland, Victoria and South Australia for males – and the same group for females, except Java). Examination of the residuals from regression analysis gave no indication of heteroscedasticity. Because of the number of associations being tested in the multiple regression analysis the level of significance was set at P<0.01,

Stepwise canonical variate (discriminant function) analyses (DFA) were run for all skull, dentary and dental characters for males and females combined after first testing for sexual dimorphism. External measurements were

analysed separately from these other characters and localities were grouped following the groups indicated by the DFA of the skull, dentary and dental characters. In all instances DFA was run using all characters and each island as a group. These islands were then placed into broader groups and the DFA repeated using all characters and these new broad groupings. From this latter

Table 1 Multiple regression on sex and locality (see text) of *Myotis* for (a) skull, dentary and dental characters and (b) external characters. F values are presented for the main effects and their interactions. For explanation of character codes see Materials and Methods section. Probability levels are *, 0.05>p>0.01; **, 0.01>p>0.001; and ***, p<0.001.

Table 1a			
Character	Main Effects		Interaction
	Sex	Location	Sex. Location
GSL	0.066	24.034***	0.472
CBL	0.716	21.410***	0.485
BB	0.828	27.613***	0.527
MW	0.675	17.075***	0.671
CH	0.130	10.944***	1.053
RL	0.556	15.126***	0.524
AOB	0.365	11.587***	1.539
LIB	4.828*	11.956***	1.723
PPL	3.744	10.593***	1.667
MFB	6.091*	6.262***	2.429*
BUL	0.396	9.946***	1.518
C'C'W	0.239	2.519*	0.400
M ³ M ³ W	1.476	25.723***	0.685
C ¹ M ³ L	2.563	26.264***	0.856
I ¹ M ³ L	2.504	24.405***	0.743
M ² B	0.948	2.389*	0.448
ANRAM	0.000	14.651***	0.453
DL	0.163	23.486***	1.181
I ₁ M ₃ L	1.230	25.747***	1.206
d.f.	1,87	9,87	9,87

Table 1b			
Character	Main Effects		Interaction
	Sex	Location	Sex. Location
SVL	0.987	3.003**	1.142
TV	0.745	12.689***	1.228
EL	0.005	41.009***	0.786
TIB	5.011*	35.391***	1.854
PES	0.038	25.312***	1.009
FA	11.784**	48.818***	1.027
D3M	11.059**	36.414***	1.157
D3P1	7.668**	73.116***	1.992
D3P2	2.917	35.852***	1.069
D4M	9.448**	33.668***	1.460
D4P1	6.556*	26.135***	1.062
D4P2	1.400	10.579***	0.653
D5M	9.713**	34.009***	1.677
D5P1	6.915*	8.008***	1.083
d.f.	1,91	8,91	8,91

Table 2 Measurements, in mm, for (a) skull, dentary and dental characters, and (b) external characters (see Materials and Methods for explanation of character codes) of adult *Myotis adversus* (all populations); *M. a. adversus* (Java I; Kangean Is, Nusa Penida I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Timor I., Savu I.); *M. a. tanimbarensis* subsp. nov. (Yamdena I.); *M. a. wetarensis* subsp. nov. (Wetar I.); *Myotis adversus* subsp. indet. (New South Wales); *Myotis moluccarum* (all populations); *M. m. moluccarum* (Western Australia, Papua New Guinea, Seram I.); *M. m. richardsi* subsp. nov. (Queensland, Northern Territory); *M. moluccarum* (Solomon Is) and *Myotis macropus* (Victoria, South Australia). N = sample size; SD = standard deviation; MIN = minimum; and MAX = maximum.

Table 2a		GSL	CBL	BB	ZW	MW	CH	RL	AOB	LIB
Taxon										
<i>Myotis adversus</i> (all populations)	N	73	73	73	63	73	73	73	73	73
	MEAN	16.55	15.13	8.11	10.40	8.56	6.35	4.85	4.48	4.06
	SD	0.30	0.30	0.13	0.21	0.17	0.13	0.17	0.14	0.10
	MIN	15.72	14.47	7.70	9.60	8.08	5.89	4.34	4.12	3.85
	MAX	17.20	15.85	8.40	10.75	8.91	6.64	5.22	4.76	4.31
<i>Myotis adversus</i> <i>adversus</i>	N	46	46	46	45	46	46	46	46	46
	MEAN	16.58	15.10	8.14	10.43	8.58	6.36	4.85	4.44	4.06
	SD	0.25	0.25	0.12	0.18	0.17	0.13	0.14	0.11	0.11
	MIN	15.79	14.59	7.87	9.81	8.19	6.06	4.50	4.12	3.85
	MAX	17.13	15.68	8.40	10.75	8.91	6.64	5.13	4.72	4.31
<i>Myotis adversus</i> <i>tanimbarensis</i>	N	8	8	8	3	8	8	8	8	8
	MEAN	16.14	14.79	8.07	10.07	8.29	6.22	4.65	4.45	4.06
	SD	0.28	0.27	0.17	0.40	0.13	0.14	0.21	0.12	0.11
	MIN	15.72	14.47	7.70	9.60	8.08	5.89	4.34	4.32	3.87
	MAX	16.66	15.31	8.27	10.30	8.52	6.35	4.92	4.66	4.08
<i>Myotis adversus</i> <i>wetarensis</i>	N	18	18	18	14	18	18	18	18	18
	MEAN	16.71	15.37	8.04	10.43	8.62	6.38	4.94	4.61	4.12
	SD	0.23	0.24	0.11	0.11	0.09	0.11	0.15	0.16	0.07
	MIN	16.34	14.92	7.81	10.21	8.49	6.20	4.66	4.16	4.01
	MAX	17.20	15.85	8.25	10.62	8.83	6.61	5.22	4.76	4.26
<i>Myotis adversus</i> subsp. indet	N=1	15.94	14.64	8.16	9.74	8.53	6.25	4.67	4.48	3.97
<i>Myotis moluccarum</i> (all populations)	N	37	37	37	34	37	37	37	37	37
	MEAN	15.64	14.48	7.81	10.06	8.24	6.08	4.46	4.22	3.85
	SD	0.34	0.38	0.18	0.30	0.24	0.18	0.17	0.14	0.12
	MIN	14.98	13.80	7.48	9.50	7.90	5.82	4.17	3.89	3.53
	MAX	16.37	15.39	8.19	10.76	8.91	6.59	4.92	4.51	4.20
<i>Myotis moluccarum</i> <i>moluccarum</i>	N	22	22	22	22	22	22	22	22	22
	MEAN	15.48	14.29	7.70	9.92	8.13	6.01	4.36	4.16	3.87
	SD	0.23	0.19	0.10	0.20	0.15	0.13	0.11	0.08	0.09
	MIN	14.98	13.97	7.48	9.50	7.90	5.84	4.17	4.00	3.71
	MAX	15.82	14.59	7.86	10.28	8.41	6.32	4.62	4.32	4.07
<i>Myotis moluccarum</i> <i>richardsi</i>	N	13	13	13	13	13	13	13	13	13
	MEAN	15.95	14.87	8.01	10.32	8.49	6.17	4.62	4.36	3.88
	SD	0.31	0.35	0.11	0.28	0.23	0.23	0.15	0.09	0.13
	MIN	15.39	14.27	7.85	9.74	8.12	5.82	4.38	4.21	3.71
	MAX	16.37	15.39	8.19	10.76	8.91	6.59	4.92	4.51	4.20
<i>Myotis moluccarum</i> (Solomon Is)	N	2	2	2	2	2	2	2	2	2
	MEAN	15.33	14.00	7.69	9.75	8.01	6.10	4.37	3.91	3.64
	SD	0.36	0.28	0.18	0.17	0.11	0.04	0.09	0.03	0.06
	MIN	15.07	13.80	7.56	9.63	7.93	6.07	4.30	3.89	3.59
	MAX	15.58	14.20	7.82	9.87	8.09	6.12	4.43	3.93	3.68
<i>Myotis macropus</i>	N	15	15	15	12	15	15	15	15	15
	MEAN	16.75	15.66	8.36	10.70	8.70	6.46	4.84	4.58	4.05
	SD	0.46	0.46	0.17	0.38	0.18	0.22	0.21	0.21	0.11
	MIN	16.18	14.91	8.14	10.20	8.48	6.19	4.51	4.32	3.88
	MAX	17.76	16.58	8.70	11.42	9.15	6.87	5.23	5.03	4.20

Table 2a (continued)

PPL	MFB	BUL	C'C'W	M³M³W	I'M³L	C'M³L	M²B	AMRAM	DL	I,M₃L
73	73	73	73	73	73	73	73	73	73	73
5.43	2.26	2.96	4.61	6.80	7.34	6.20	1.73	4.38	12.04	7.90
0.12	0.11	0.11	0.12	0.17	0.17	0.14	0.06	0.15	0.23	0.18
5.17	1.98	2.69	4.33	6.32	7.01	5.90	1.58	4.02	11.43	7.44
5.70	2.52	3.18	4.87	7.06	7.75	6.43	1.87	4.70	12.54	8.20
46	46	46	46	46	46	46	46	46	46	46
5.41	2.28	2.96	4.62	6.82	7.34	6.22	1.71	4.42	12.06	7.93
0.14	0.10	0.09	0.11	0.14	0.14	0.12	0.05	0.15	0.20	0.16
5.19	2.11	2.82	4.33	6.57	7.01	5.92	1.58	4.02	11.63	7.54
5.67	2.52	3.17	4.87	7.06	7.61	6.43	1.79	4.70	12.54	8.18
8	8	8	8	8	8	8	8	8	8	8
5.41	2.27	2.96	4.61	6.82	7.34	6.04	1.70	4.41	12.05	7.94
0.14	0.11	0.10	0.12	0.14	0.14	0.14	0.05	0.15	0.21	0.15
5.30	1.98	2.72	4.34	6.32	7.03	5.90	1.62	4.03	11.43	7.44
5.51	2.28	2.98	4.77	6.70	7.37	6.32	1.79	4.36	12.12	7.90
18	18	18	18	18	18	18	18	18	18	18
5.49	2.31	3.01	4.63	6.89	7.45	6.25	1.79	4.39	11.70	7.64
0.10	0.07	0.11	0.11	0.09	0.14	0.11	0.04	0.13	0.23	0.15
5.17	2.11	2.69	4.44	6.70	7.22	6.06	1.74	4.13	11.43	7.44
5.70	2.42	3.18	4.85	7.02	7.75	6.43	1.87	4.50	12.12	7.90
5.38	2.08	3.13	4.46	6.60	7.04	5.96	1.62		11.73	7.64
37	37	33	37	37	37	37	37	37	37	37
5.29	2.14	2.82	4.49	6.41	6.92	5.88	1.66	4.15	11.52	7.56
0.14	0.08	0.14	0.10	0.14	0.15	0.17	0.07	0.21	0.33	0.20
4.97	1.90	2.58	4.22	6.19	6.68	5.66	1.41	3.77	11.06	7.30
5.62	2.28	3.07	4.68	6.76	7.32	6.38	1.80	4.74	12.32	8.15
22	22	22	22	22	22	22	22	22	22	22
5.28	2.13	2.77	4.50	6.36	6.85	5.79	1.65	4.03	11.32	7.46
0.12	0.06	0.10	0.08	0.10	0.10	0.08	0.07	0.09	0.18	0.11
4.97	2.01	2.58	4.40	6.19	6.68	5.66	1.41	3.77	11.06	7.30
5.51	2.23	3.01	4.68	6.58	7.06	5.96	1.79	4.21	11.69	7.71
13	13	9	13	13	13	13	13	13	13	13
5.34	2.17	2.96	4.50	6.51	7.03	6.03	1.68	4.35	11.86	7.74
0.14	0.08	0.12	0.11	0.16	0.16	0.18	0.08	0.22	0.27	0.23
5.11	2.08	2.77	4.33	6.26	6.74	5.77	1.58	4.00	11.43	7.35
5.62	2.28	3.07	4.67	6.76	7.32	6.38	1.80	4.74	12.32	8.15
2	2	2	2	2	2	2	2	2	2	2
5.05	1.97	2.62	4.28	6.31	6.83	5.82	1.67	4.08	11.20	7.40
0.07	0.09	0.06	0.08	0.01	0.13	0.11	0.05	0.21	0.17	0.12
5.00	1.90	2.58	4.22	6.30	6.74	5.74	1.63	3.93	11.08	7.31
5.10	2.03	2.66	4.34	6.31	6.92	5.90	1.70	4.23	11.32	7.48
15	15	15	15	15	15	15	15	15	15	15
5.67	2.26	3.05	4.63	6.94	7.54	6.42	1.71	4.50	12.39	8.18
0.17	0.09	0.12	0.22	0.21	0.24	0.19	0.11	0.16	0.36	0.24
5.35	2.13	2.85	4.35	6.64	7.13	6.12	1.56	4.23	11.87	7.79
5.95	2.44	3.27	5.18	7.37	7.93	6.76	1.89	4.83	13.10	8.60

Table 2b

Taxon		SVL	TV	EL	TIB	PES	FA	D3M	D3P1	D3P2	D4M	D4P1	D4P2	D5M	D5P1
<i>Myotis adversus</i> (all populations)	N	71	71	71	71	71	71	71	71	71	71	71	71	71	71
	MEAN	48.2	42.4	16.7	19.0	11.5	42.6	41.8	17.8	16.1	40.4	11.7	10.3	38.9	10.0
	SD	2.6	3.4	0.8	0.7	0.5	1.4	1.6	0.9	0.9	1.6	0.6	0.8	1.4	0.5
	MIN	42.6	33.4	14.1	16.1	10.2	38.0	37.6	15.5	13.2	35.4	9.6	8.3	34.4	8.8
	MAX	55.0	48.4	18.2	20.6	12.5	45.2	44.6	20.2	18.2	42.8	13.4	12.1	41.8	11.6
<i>Myotis adversus</i> <i>adversus</i>	N	46	46	46	46	46	46	46	46	46	46	46	46	46	46
	MEAN	48.4	43.1	17.1	19.0	11.7	42.4	41.7	18.0	16.2	40.4	11.8	10.4	39.1	10.1
	SD	2.5	2.8	0.6	0.6	0.5	1.1	1.3	0.8	0.8	1.3	0.5	0.8	1.2	0.5
	MIN	43.3	35.7	15.5	17.4	10.7	40.1	38.2	16.2	14.7	37.1	10.7	8.4	36.0	9.0
	MAX	55.0	48.4	18.2	20.0	12.5	44.4	44.4	20.2	18.2	42.8	13.4	12.1	41.8	11.6
<i>Myotis adversus</i> <i>tanimbarensis</i>	N	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	MEAN	46.8	36.6	15.6	18.5	11.0	41.2	39.7	16.7	14.7	38.4	11.0	9.2	36.7	9.2
	SD	2.8	3.0	0.3	0.4	0.6	1.1	1.4	0.5	0.6	1.6	0.5	0.5	1.4	0.4
	MIN	42.6	33.4	15.2	18.0	10.2	39.9	37.6	16.1	13.9	35.9	10.3	8.5	35.1	8.8
	MAX	49.9	40.1	16.1	19.3	11.8	43.2	42.1	17.3	15.3	40.9	11.6	9.7	39.3	9.8
<i>Myotis adversus</i> <i>wetarensis</i>	N	17	17	17	17	17	17	17	17	17	17	17	17	17	17
	MEAN	48.3	43.2	16.4	19.5	11.3	43.8	43.1	18.1	16.5	41.3	11.7	10.6	39.6	9.9
	SD	2.9	3.0	0.4	0.6	0.4	0.8	0.9	0.6	0.6	0.9	0.3	0.6	0.8	0.3
	MIN	42.7	36.2	15.8	18.7	10.8	42.3	41.4	16.8	15.6	39.6	11.0	9.2	38.5	9.5
	MAX	51.5	47.1	17.4	20.6	12.0	45.2	44.6	18.7	17.7	42.5	12.2	11.6	40.7	10.4
<i>Myotis adversus</i> subsp. indet.	N=1	49.3	39.6	14.1	16.1	10.5	38.0	37.8	15.5	13.2	35.4	9.6	8.3	34.4	9.0
<i>Myotis</i> <i>moluccarum</i> (all populations)	N	37	37	37	37	37	37	37	37	37	37	37	37	36	37
	MEAN	45.0	38.1	15.1	16.7	9.8	38.2	37.2	14.2	13.4	36.6	10.1	8.7	35.4	9.3
	SD	3.3	2.1	0.6	0.6	0.5	1.2	1.1	0.6	0.8	0.9	0.5	0.7	0.9	0.3
	MIN	34.8	34.3	13.8	15.6	8.6	35.4	34.0	12.7	11.2	35.0	9.0	6.7	33.7	8.6
	MAX	54.3	42.4	16.0	18.1	11.0	41.0	39.1	15.7	15.2	38.5	11.5	10.3	37.1	10.2
<i>Myotis</i> <i>moluccarum</i> <i>moluccarum</i>	N	22	22	22	22	22	22	22	22	22	22	22	22	21	22
	MEAN	45.2	38.1	15.4	16.7	9.9	37.7	36.8	14.1	13.1	36.3	10.1	8.8	35.2	9.3
	SD	2.0	2.1	0.5	0.6	0.6	1.1	1.2	0.6	0.6	0.8	0.4	0.6	0.8	0.4
	MIN	41.2	34.3	14.2	15.6	8.6	35.4	34.0	12.7	11.2	35.0	9.0	7.9	33.7	8.6
	MAX	49.0	42.1	16.0	18.1	10.8	39.7	38.4	15.1	14.1	37.6	10.8	10.3	36.6	9.9
<i>Myotis</i> <i>moluccarum</i> <i>richardsi</i>	N	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	MEAN	45.5	37.9	14.6	16.8	9.8	38.8	37.7	14.2	13.5	37.0	10.1	8.6	35.6	9.4
	SD	4.1	2.3	0.5	0.5	0.5	1.1	0.9	0.5	0.9	0.9	0.3	0.8	1.1	0.3
	MIN	37.1	35.3	13.8	16.1	9.0	37.0	35.8	13.4	11.8	35.3	9.4	6.7	33.7	9.0
	MAX	54.3	42.4	15.2	17.8	11.0	41.0	39.1	15.0	15.2	38.5	10.5	9.9	37.1	10.2
<i>Myotis</i> <i>moluccarum</i> (Solomon Is)	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	MEAN	39.1	37.5	14.7	16.7	9.8	39.6	37.3	15.0	14.2	36.2	10.6	8.4	35.3	9.3
	SD	6.2	3.5	0.1	0.3	0.4	1.1	1.1	0.9	0.3	1.6	0.4	0.0	1.4	0.3
	MIN	34.8	35.1	14.6	16.5	9.5	38.8	36.5	14.4	14.0	35.1	10.3	8.4	34.3	9.1
	MAX	43.5	40.0	14.7	17.0	10.0	40.4	38.1	15.7	14.5	37.3	10.8	8.4	36.2	9.5
<i>Myotis macropus</i>	N	13	13	13	13	13	13	13	13	13	13	13	13	13	13
	MEAN	47.1	38.8	15.2	17.5	11.0	40.3	39.4	14.8	14.1	38.3	10.4	9.3	36.9	9.8
	SD	2.6	2.3	0.5	0.5	0.7	1.1	1.2	0.7	0.5	1.34	0.7	0.9	1.1	0.4
	MIN	41.7	34.4	14.3	16.5	9.9	38.2	37.2	13.7	13.1	36.7	9.1	6.6	35.0	9.4
	MAX	50.5	43.4	15.8	18.3	12.3	41.8	41.1	15.8	14.9	40.5	11.4	10.0	38.2	10.7

analysis a reduced set of 5–10 characters was selected. It is the DFA based on this reduced set of characters that is discussed in the text, because in all instances they provided similar discriminant function plots to those of the complete set of characters. These reduced set of characters were selected in all these analyses because the sample size of the smallest *a priori* group selected approximated, or was less than, the number of characters in the analysis. This reduced set of characters was chosen because they provided values that minimise Wilk's lambda. The statistical software used throughout was SPSS PC+.

RESULTS AND DISCUSSION

Univariate statistics

Multiple regressions were run separately for skull, dentary and dental characters, excluding zygomatic width which was missing values from many specimens, and external characters because these analyses utilised different sets of locations and sample sizes.

Skull, dentary and dental characters

Sex. No characters were significantly influenced by sex alone, although least interorbital breadth and mesopterygoid fossa breadth were weakly associated with sex ($F_{1,87} = 4.828$; $P = 0.031$ and $F_{1,87} = 6.091$; $P = 0.016$, respectively) (Table 1a).

Location. All characters, except C'C' width and M² breadth were very significantly ($P < 0.001$) influenced by location alone (Table 1a).

Interaction. There were no significant interactions, although there was a weak interaction between sex and location for mesopterygoid fossa breadth ($F_{9,87} = 2.429$; $P = 0.016$) (Table 1a).

External characters

Sex. A number of characters representing wing size were influenced by sex alone, with females being larger than males. These characters were forearm length ($F_{1,91} = 11.784$; $P = 0.001$); digit 3 metacarpal length ($F_{1,91} = 11.059$; $P = 0.001$); digit 3 phalanx 1 length ($F_{1,91} = 7.668$; $P = 0.007$); digit 4 metacarpal length ($F_{1,91} = 9.448$; $P = 0.003$); and digit 5 metacarpal length ($F_{1,91} = 9.713$; $P = 0.003$) (Table 1b).

Location. All characters were significantly ($P < 0.001$) influenced by location alone. The lack of significant interaction between sex and location indicates that the relationship between wing size of male and females was consistent for all locations.

Mean, standard deviation, minimum and maximum values and sample size for each locality are presented in Table 2 for skulls, dentary and dental characters (2a) and external body characters

(2b) for all characters examined for the locations or location groupings determined in this study to have taxonomic significance. Values for males and females are combined for both the skull, dental and dentary characters and for the external characters. Although most of the wing measurements for females were larger than those of the males, these differences were generally greatly exceeded by the differences between islands or groups of islands.

Multivariate analyses

In the subsequent DFA of skull, dentary, dental and external characters, males and females were combined. This is appropriate for the skull, dentary and dental characters because they were not significantly influenced by sex. It is less satisfactory for the external characters because many of the wing measurements were influenced by sex. For this reason, the location groupings (possibly representative of putative taxa) were selected on the basis of the skull, dentary and dental characters. The external characters were then placed into location groupings as for the skull and other characters. It was considered that the loss of distinction between the recognised island groupings, or taxa, based on their external measurements, would be minimal because location differences far exceeded sex differences for most of the external characters (Table 1b).

All locations – skull, dentary and dental characters

DFA was run on a reduced set of 10 selected characters (listed in Table 3a) for all locations. Three groupings of locations were apparent. These were:

- (i) The Lesser Sunda Group (Java I., Kangean I., Nusa Penida I., Sumbawa I., Moyo I., Flores I., Lembata I., Pantar I., Alor I., Wetar I., Yamdena I., Timor I., Savu I., New South Wales);
- (ii) The Western Australian Group (Western Australia, Northern Territory, Queensland, Seram, Papua New Guinea and Solomon Islands); and
- (iii) The Victorian Group (Victoria, South Australia).

A DFA using the above 10 characters and these three *a priori* groupings extracted two highly significant Functions. Function 1 explained 72.2% of the variance and Function 2, 27.8%.

A total of 97.6% of individuals were classified to their correct group. Misclassifications were in the Lesser Sunda Group, with one specimen from this group allocating to the Victorian Group and two specimens to the Western Australian Group.

Function 1 separated both the Lesser Sunda Group and the Victorian Group from the Western Australian Group (Figure 2a). The characters

Table 3 Canonical Variate Function coefficients for the three locality groups: Lesser Sunda; Western Australian; and Victorian (see text for clarification). Standardised values followed by (in brackets) unstandardised values for (a) 10 skull and dental characters and (b) seven external characters. For explanation of character codes see Materials and Methods section.

Table 3a

Character	Function 1		Function 2	
M ³ M ³ W	0.5469	(3.3069)	0.1786	(1.0802)
BB	0.0790	(3.1840)	0.4706	(3.1285)
LIB	0.1569	(1.4119)	-0.1350	(-1.2154)
PPL	0.3856	(2.8807)	0.0581	(0.4341)
C ¹ C ¹ W	-0.5574	(-4.2458)	0.0018	(0.0134)
GSL	1.2016	(3.5616)	-1.8370	(-5.4449)
CBL	-1.9381	(-5.5309)	2.1724	(6.1994)
RL	0.1723	(0.9570)	-0.9471	(-5.2606)
I ¹ M ³ L	0.7461	(4.3581)	0.5446	(3.1809)
M ² B	-0.0812	(-1.1189)	-0.4262	(-5.8712)
Constant	-58.8462		-22.3024	
Variance Explained (%)	72.2		27.8	

Table 3b

Character	Function 1		Function 2	
D3P1	0.5373	(0.7249)	-0.7477	(-1.0087)
FA	0.0894	(-0.0752)	0.8681	(0.7301)
D5P2	0.4108	(-0.9332)	0.6058	(1.3762)
TIB	0.3731	(0.6049)	-0.3616	(-0.5862)
D3P2	0.3885	(0.5117)	-0.1650	(-0.2174)
D3M	-0.0544	(-0.0414)	0.4549	(0.3458)
EL	0.3825	(0.5846)	0.0720	(0.1100)
Constant	-35.8578		-23.6352	
Variance Explained (%)	94.6		5.4	

loading most heavily (>0.5) on this Function were: condylobasal length; greatest skull length; I¹M³ length; C¹C¹ width; and M³M³ breadth (Table 3a). Function 2 separated the Victorian Group from both the Lesser Sunda Group and the Western Australian Group. The characters loading most heavily (>0.5) on this Function were: condylobasal length; greater skull length; rostrum length; and I¹M³ length (Table 3a). It appears that the Western Australian Group will be distinguished from the other two groups on overall size, particularly skull length, palatal breadth and tooth row length. The Victoria Group separated from the other two groups on a shape difference involving the relationship between condylobasal and greatest skull length, and tooth row length. The Lesser Sunda Group separated from the other two groups on a combination of the above characters.

All locations – external characters

DFA was run on a reduced set of seven

characters (listed in Table 3b) using the three above location groupings determined for the skull, dentary and dental characters. This DFA extracted two very significant Functions (Figure 2b). Function 1 explained 94.6% of the variance and Function 2, 5.4%. A total of 95.5% of individuals were classified to their correct group; two specimens from the Victorian Group were misclassified to the Western Australian Group and three specimens from this latter group were misclassified to the Victorian Group.

Function 1 separated the Lesser Sunda Group from both the Western Australian and Victorian Groups. The character loading most heavily (>0.5) on Function 1 was digit 3 phalanx 1 length (Table 3b). Function 2 partially separated the Victorian and Western Australian Groups. The characters loading most heavily (>0.5) on Function 2 were: forearm length; digit 3 phalanx 1 length; and digit 5 phalanx 2 length. (Table 3b). This suggested that these three groups can be separated by aspects of the wing structure, particularly digit 3 phalanx 1 length.

The Lesser Sunda Group – skull and dental characters

DFA was run on a reduced set of five skull and dental characters (listed in Table 4a) for all island locations in the Javan Group. Three groupings of islands were apparent. These were:

- (i) The Alor Group (Java, Kangean, Nusa Penida, Sumbawa, Moyo, Flores, Lembata, Pantar, Alor, Timor and Savu);
- (ii) Wetar; and
- (iii) Yamdena.

The single New South Wales specimen was left unallocated.

A DFA, using both the above five characters and the three above *a priori* island groupings, extracted two very significant Functions. Function 1 explained 65.1% of the variance and Function 2, 34.9%. A total of 88.9% of specimens were allocated to their correct group. Misclassifications were as follows: Two of the Alor Group were misclassified to Yamdena; three to Wetar. Two from Wetar were misclassified to the Alor Group and one to Yamdena.

The single specimen from New South Wales was classified to the Yamdena population.

Function 1 almost completely separated the Alor Group from the Yamdena population (Figure 3a). The characters loading heavily (>0.5) on Function 1 were M³M³ width; anteorbital foramen breadth; M² breadth; and mesopterygoid fossa breadth (Table 4a). Function 2 partially separates the Wetar population from both the Alor Group and the Yamdena population (Figure 3a). The character loading heavily on Function 2 was M² breadth.

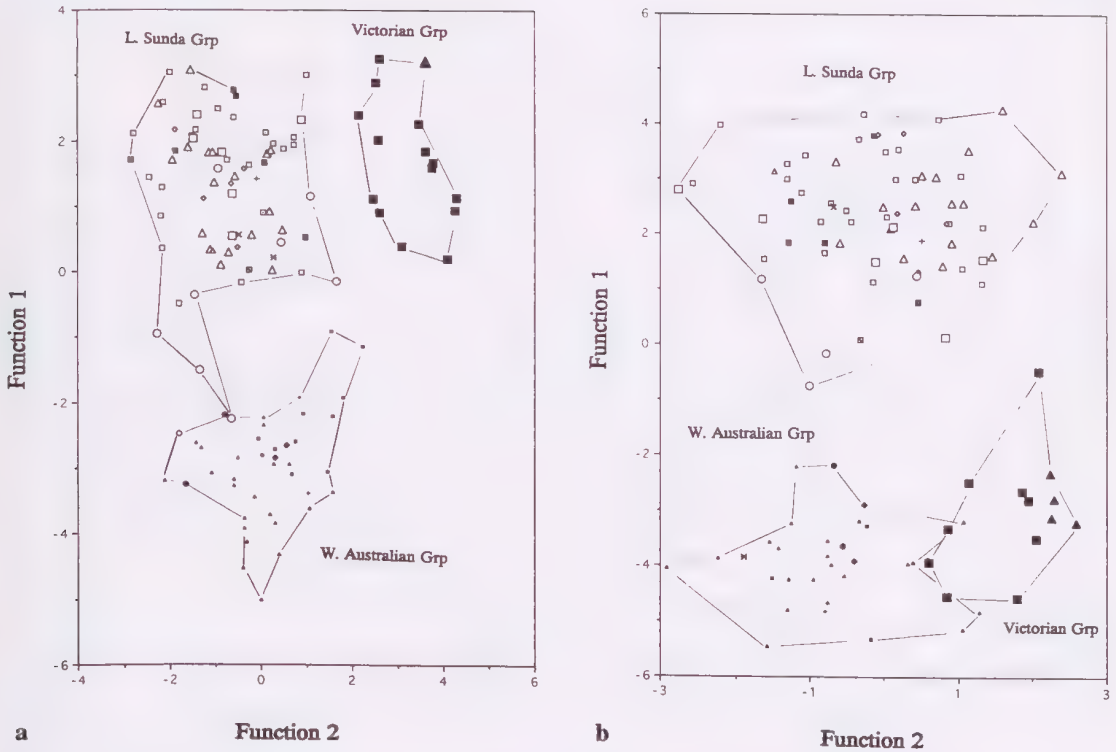


Figure 2 Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined and based on three locality groups: Lesser Sunda, Western Australian and Victorian (see text for clarification) for (a) 10 skull, dental and dentary characters; and (b) seven external characters. Locality codes are as follows: \square , Alor I.; \blacklozenge , Papua New Guinea; \square , Savu I.; \diamond , Sumbawa I.; $+$, Northern Territory; \square , Flores I.; \circ , Seram I.; \bullet , Solomon Is.; \boxtimes , Java I.; $+$, Kangean Is.; \boxplus , Lembata I.; \times , Moyo I.; \times , New South Wales; \boxtimes , Pantar I.; \blacksquare , Queensland; Δ , Wetar I.; \blacktriangle , South Australia; Δ , Timor I.; \blacksquare , Victoria; \blacktriangle , Western Australia; and \circ , Yamdena I.

The Lesser Sunda Group – externals

DFA was run on a reduced set of five characters (listed in Table 4b) using the above three island groupings that were determined for the skull, dentary and dental characters. This DFA extracted two very significant Functions. Function 1 explained 61.7% of the variation and Function 2, 38.3%. A total of 88.2% of individuals were classified to their correct island group. Misclassifications were as follows: Three individuals from the Alor Group to the Yamdena population, four individuals from the Alor Group to the Wetar population; and one individual from the Wetar Group to the Yamdena population. All Yamdena individuals were correctly classified. Function 1 partially separated the Yamdena population from both the Alor Group and the Wetar population (Fig 3b). The character loading heavily (>0.5) on Function 1 was ear length (Table 4b). Function 2 separated the Yamdena and Wetar populations (Fig. 3b). The character loading heavily (>0.5) on Function 2 was forearm length (Table 4b).

The Western Australian Group – skull, dentary and dental characters

DFA was run on all characters, except zygomatic breadth (missing in a number of specimens), for all locations. Four groups were identified. These groups were:

- (i) Western Australia;
- (ii) Queensland and Northern Territory;
- (iii) Solomons; and
- (iv) Papua New Guinea and Seram

The DFA run with these four groups and using all characters, extracted two significant Functions. Function 1 explained 67.4% of the variance and Function 2, 28.7% (Figure 4a). A total of 95% of individuals were classified to their correct group. Misclassifications were in the Queensland/NT Group, where one specimen classified to Western Australia and one to the Papua New Guinea/Seram Group.

A DFA was run again using a reduced set of five characters (dentary length, anteorbital foramen

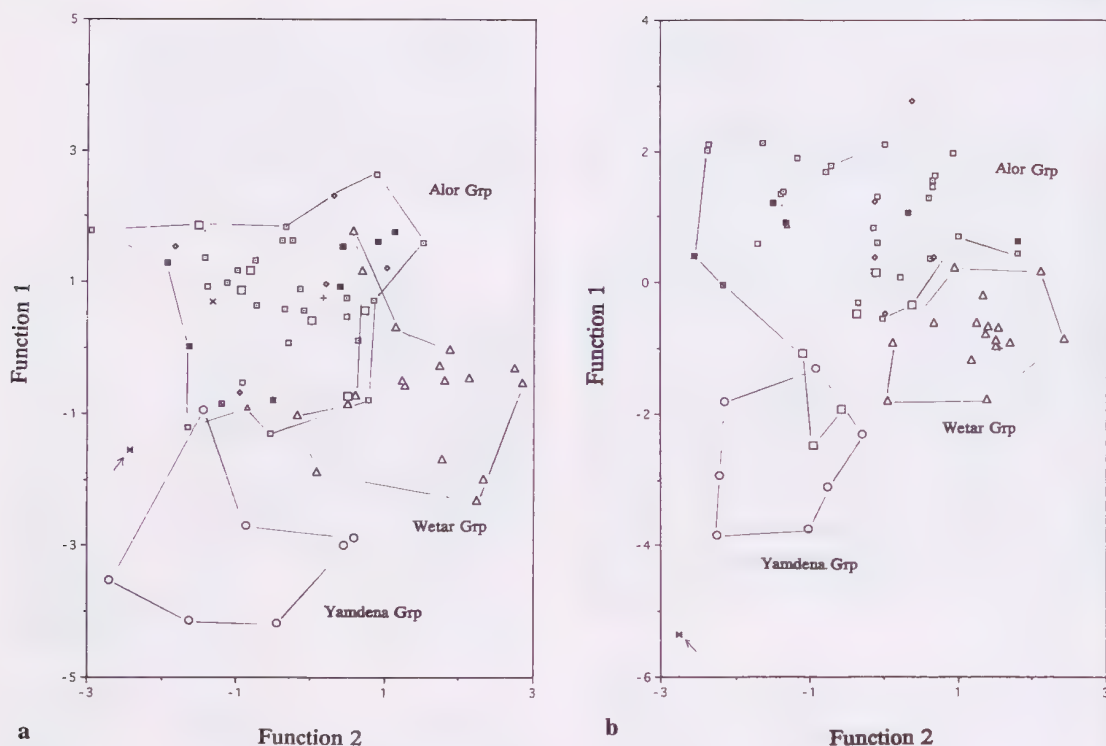


Figure 3 Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined, based on the following three island groups in the Lesser Sundas: Alor, Wetar and Yamdena. The NSW specimen (arrowed) was unallocated (see text for clarification) for (a) five skull and dental characters and (b) five external characters. Locality codes as for Figure 2 captions.

width, M^2 breadth, least interorbital breadth, $C'C^1$ width) selected from the above analysis and using the Western Australia and Queensland/Northern Territory Groups only. The Solomon Island sample ($N=2$) and the Papua New Guinea/Seram sample ($N=3$) were too small to include as groups – so these latter specimens were included in this analysis as unallocated specimens. This analysis extracted a highly significant function with 97.1% of individuals classified to their correct group. Only one specimen was misclassified between these two groups: one from the Western Australian Group was misclassified to the Queensland/NT Group (Figure 5a). On this Function the two Solomon Island specimens allocated to the Western Australian Group while the PNG/Seram individuals were intermediate. The characters loading heavily (>0.5) on Function 1 and which were influential in discriminating between the Western Australian Group and the Queensland/NT Group were anteorbital foramen width, dentary length and $C'C^1$ width (Table 5a).

The Western Australian Group – externals

A DFA was run on all characters for the island groupings identified in the earlier DFA analysis on

skull, dentary and dental characters (WA, Qld/NT, Solomons, PNG/Seram). This latter analysis extracted two significant Functions. Function 1 explained 77.6% of the variance, and Function 2 20.6% (Figure 4b). A total of 89.5% of individuals were classified to their correct group. Misclassifications were as follows: one Western Australian Group individual to the Queensland/NT Group and three of this latter group to the Western Australian Group. A DFA was again run using a reduced set of five characters (ear length, forearm length, digit 4 metacarpal length, digit 4 phalanx 2 length and digit 5 metacarpal length) selected from the above analysis and using the Western Australia and Queensland/Northern Territory Groups only. The Solomon Island sample ($N=2$) and the Papua New Guinea sample ($N=2$) were too small to include as groups – so these were included in this analysis as unallocated specimens. This analysis extracted a highly significant Function with 100% of individuals classified to their correct group. On this Function both the two Solomon Island specimens and the Papua New Guinea specimens allocated to the Queensland/NT Group (Figure 5b). The characters loading heavily (>0.5) on Function 1, and which were influential in

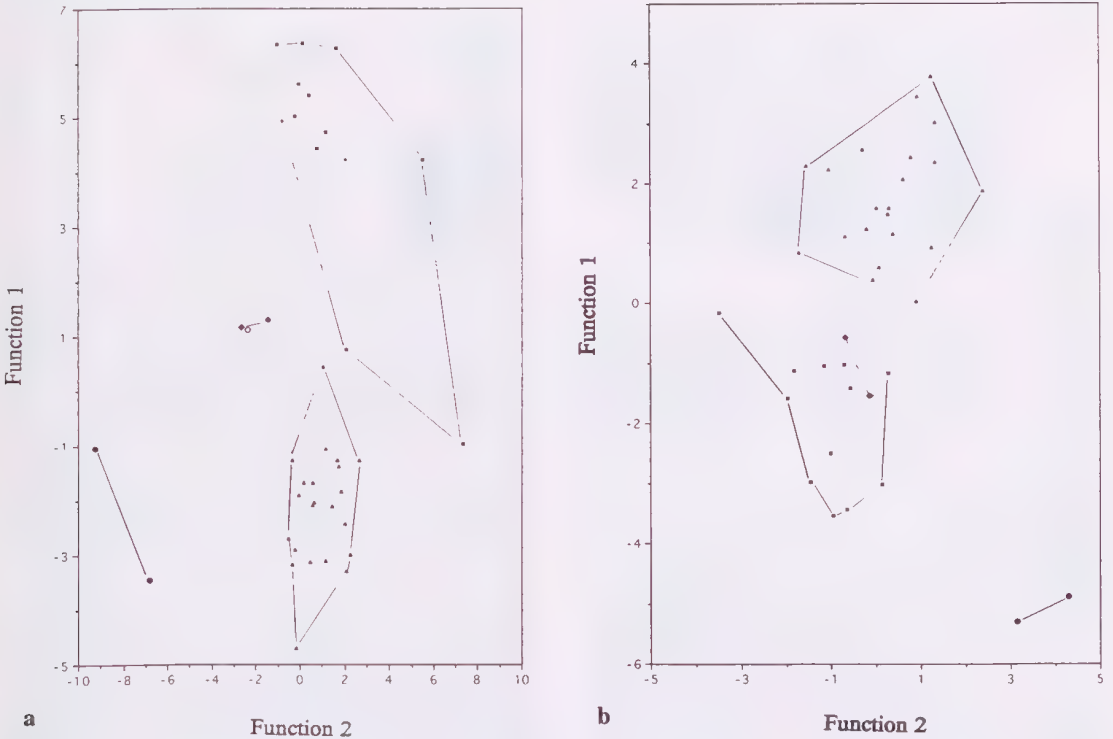


Figure 4 Plots of Functions 1 and 2 from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined based on the following four locality groupings in the Western Australian Group: Western Australia; Queensland/Northern Territory; Papua New Guinea/Seram; and Solomon Is for (a) all skull characters except zygomatic breadth, and (b) all external characters. Locality codes as for Figure 2 caption.

discriminating between the Western Australian Group and the Queensland/NT Group, were forearm length, ear length, digit 5 metacarpal length and digit 4 phalanx 2 length (Table 5b).

In summary, three broad and distinct locality groups were apparent from DFA. These were: (i) the islands of Java, Nusa Penida, Kangean, through Nusa Tenggara to the southwestern islands of Maluku Tenggara, and possibly to New South Wales; (ii) central Maluku, northern Australia, Papua New Guinea to the Solomon Islands; and (iii) southeastern Australia. Further, within the first two of these broad locality groups are a further six recognisable locality subgroups.

These locality groups and subgroups represent putative taxa. These grouped populations of *Myotis* include the following named forms of *Myotis adversus*: *adversus*; *moluccarum*; *macropus*; and *solomonis*. The following taxonomic section allocates these above named forms to their appropriate locality group, describes and rediagnosis the previously named taxa, and proposes and describes three new subspecies to represent unnamed and morphologically distinct populations.

TAXONOMY

Myotis adversus (Horsfield, 1824)

Vespertilio adversus Horsfield, 1824: 2 unnumbered pages

Diagnosis

Myotis adversus differs from *Myotis moluccarum* in averaging larger in all skull, dental and dentary characters, although none absolutely so (Table 1). For example, greatest skull length 16.55 (15.72–17.20) 73 v. 15.64 (14.98–16.37) 37; braincase breadth 8.11 (7.70–8.40) 73 v. 7.81 (7.48–8.19) 37; zygomatic width 10.40 (9.60–10.75) 63 v. 10.06 (9.50–10.76) 34; Ist PM length 7.34 (7.01–7.75) 73 v. 6.92 (6.68–7.32) 37; and dentary length 12.04 (11.43–12.54) 73 v. 11.52 (11.06–12.32) 37. Greatest skull length generally larger relative to both condylobasal length and braincase breadth (Figures 6 a,b, respectively); and Ist PM length generally greater relative to braincase breadth (Figure 7). It also averages larger in all external measurements. For example ear length 16.7 (14.1–18.2) 71 v. 15.1 (13.8–16.0) 37; tibia length 19.0 (16.1–20.6) 71 v. 16.7 (15.6–18.1) 37; forearm length 42.6 (38.0–45.2) 71 v.

Table 4 Canonical Variate Function coefficients for the three island groups in the Lesser Sundas; Alor; Wetar and Yamdena; The NSW specimen was unallocated. (see text for clarification). Standardised values followed by (in brackets) unstandardised values for (a) five skull and dental characters and (b) five external characters. For explanation of character codes see Materials and Methods section.

Character	Function 1	Function 2
M ³ M ³ W	0.7386 (5.6645)	0.1247 (0.9561)
M ² B	-0.5573 (-11.4639)	0.6636 (13.6526)
AOB	-0.6868 (-5.3612)	0.3379 (2.6373)
MFB	0.5213 (5.2694)	0.0790 (0.7985)
I ₁ M ₃	0.3722 (2.5111)	0.3305 (2.2301)
Constant	-26.4963	-61.3732
Variance		
Explained (%)	65.1	34.9

Table 4b

Character	Function 1	Function 2
EL	0.6592 (1.2682)	-0.0433 (-0.0833)
FA	-0.1511 (-0.1473)	1.0635 (1.0371)
TV	0.3056 (0.1069)	0.3314 (0.1160)
D4P1	0.3745 (0.7524)	-0.4339 (-0.8719)
PES	0.3451 (0.7368)	-0.1338 (-0.2857)
Constant	-36.7853	-34.2812
Variance		
Explained (%)	61.7	38.3

38.2 (35.4–41.0) 37; tibia length 19.0 (16.1–20.6) 71 v. 16.7 (15.6–18.1) 37; and digit 3 phalanx 1 length 17.8 (15.5–20.2) 71 v. 14.2 (12.7–15.7) 37. Forearm length and digit 3 phalanx 1 length both larger relative to digit 5 phalanx 2 length (Figures 8 a,b).

Myotis adversus differs from *Myotis macropus* in having skull, dental and dentary measurements that average smaller (except for rostrum length, least interorbital breadth and mesopterygoid fossa breadth). For example, greatest skull length 16.55 (15.72–17.20) 73 v. 16.75 (16.18–17.76) 15; brain case breadth 8.11 (7.70–8.40) 73 v. 8.36 (8.14–8.70) 15; zygomatic width 10.40 (9.60–10.75) 63 v. 10.70 (10.20–11.42) 12; greatest skull length generally larger relative to both condylobasal length and braincase breadth (Figures 6 a,b). It averages smaller in all external measurements (except digit 5 phalanx 2), and digit 3 phalanx 1 is of larger absolute size. For example, ear length 16.7 (14.1–18.2) 71 v. 15.2 (14.3–15.8) 13; tibia length 19.0 (16.1–20.6) 71 v. 17.5 (16.5–18.3) 13; forearm length 42.6 (38.0–45.2) 71 v. 40.3 (38.2–41.8) 13 and digit 3 phalanx 1 17.8 (15.5–20.2) 71 v. 14.8 (13.7–15.8) 13.

Myotis adversus adversus (Horsfield, 1824)

Vespertilio adversus Horsfield, 1824: 2 unnumbered pages

Syntypes

Include Natural History Museum, London, No. 79.11.21.123; adult female; carcass in alcohol, skull separate.

Type locality

Java Island.

Diagnosis

Myotis adversus adversus differs from *Myotis adversus tanimbarensis* subsp. nov. in having skull, dental and dentary measurements averaging larger, except anteorbital foramen width (Table 1). For example, greatest skull length 16.58 (15.79–17.13) 46 v. 16.14 (15.72–16.66) 8; zygomatic width 10.43 (9.81–10.75) 45 v. 10.07 (9.60–10.30) 3; I₁M₃ length 7.34 (7.01–7.61) 46 v. 7.34 (7.03–7.37) 8. M³M³ breadth generally larger relative to anteorbital foramen width (Figure 9). It also differs in having all external measurements averaging larger. For example, ear length 17.1 (15.5–18.2) 46 v. 15.6 (15.2–16.1) 7; forearm length 42.4 (40.1–44.4) 46 v. 41.2 (39.9–43.2) 7 digit 5 metacarpal length 39.1 (36.0–41.8) 46 v. 36.7 (35.1–39.3) 7. Ear length larger relative to pes length (Figure 10).

Myotis adversus adversus differs from *Myotis adversus wetarensis* subsp. nov. in having a generally longer ear 17.1 (15.5–18.2) 46 v. 16.4 (15.8–17.4) 17; generally shorter tibia 19.0 (17.4–20.0) 46 v. 19.5 (18.7–20.6) 17; forearm length 42.4

Table 5 Canonical Variate Function coefficients for the two locality groups: Western Australia and Queensland/Northern Territory (Solomon Island, Papua New Guinea and Seram specimens were unallocated in the analysis). Standardised values followed by (in brackets) unstandardised values for (a) five skull, dental and dental characters and (b) five external characters. For explanation of character codes see Materials and Methods section.

Table 5a

Character	Function 1
AOB	1.0628 (12.4574)
DL	0.9365 (4.3094)
C ¹ C ¹ W	-0.5684 (-6.2501)
M ² B	-0.4277 (-5.6417)
Constant	-64.8959

Table 5b

Character	Function 1
EL	1.0160 (2.3247)
FA	-1.3872 (-1.3330)
D5M	0.8001 (0.8595)
D4P2	0.5285 (0.7537)
Constant	-21.4448

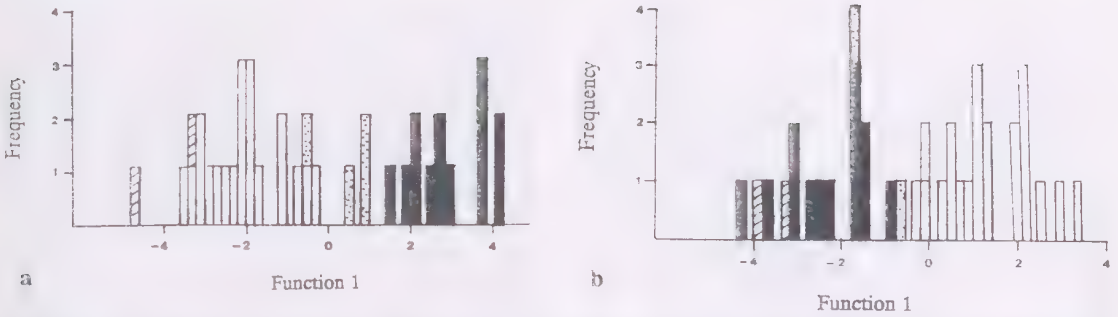


Figure 5 Histogram of Function 1 coefficients from Canonical Variate Analysis (DFA) of male and female adult *Myotis* combined, based on the two locality groupings: Western Australia, □; and Queensland/Northern Territory, ■; the Solomon Is, ▨; Papua New Guinea and Seram ▩. Specimens were unallocated for (a) five skull, dentary and dental characters and (b) five external characters.

(40.1–44.4) 46 *v.* 43.8 (42.3–45.2) 17 and digit metacarpal lengths. Anteorbital foramen width generally shorter relative to M³M³ width (Figure 9).

Description

Skull and dentition

Moderate size skull (see Table 1); rostrum rises gently posteriorly to parietal midpoint; slight sulcus in anterior part of frontal but posterior to interorbital midpoint frontal flat; cranium broad with moderate laterodorsal inflation; sagittal and lambdoidal crest absent to faint; nuchal area low domed; supraoccipital projects moderately posterior to nuchal area; infraorbital foramen oval,

with broad bar separating it from orbital cavity; zygoma moderately high and of even breadth; mesopterygoid moderately broad, partially conceals sphenorbital fissure in some specimens; anterior palate broadly incised, posterior edge of the emargination reaches almost to C¹ midpoint; palate shelf extends posterior almost to midpoint between M³ posterior edge and tympanic bulla anterior edge; palate posterior to M³ posterior edge fragile, with thin median process projecting slightly ventrally from its surface and slightly beyond its posterior margin; presphenoid usually with slight sulcus; basisphenoid with moderate anterolateral depression for cochlea.

Upper incisors bicuspid with I² size half again as

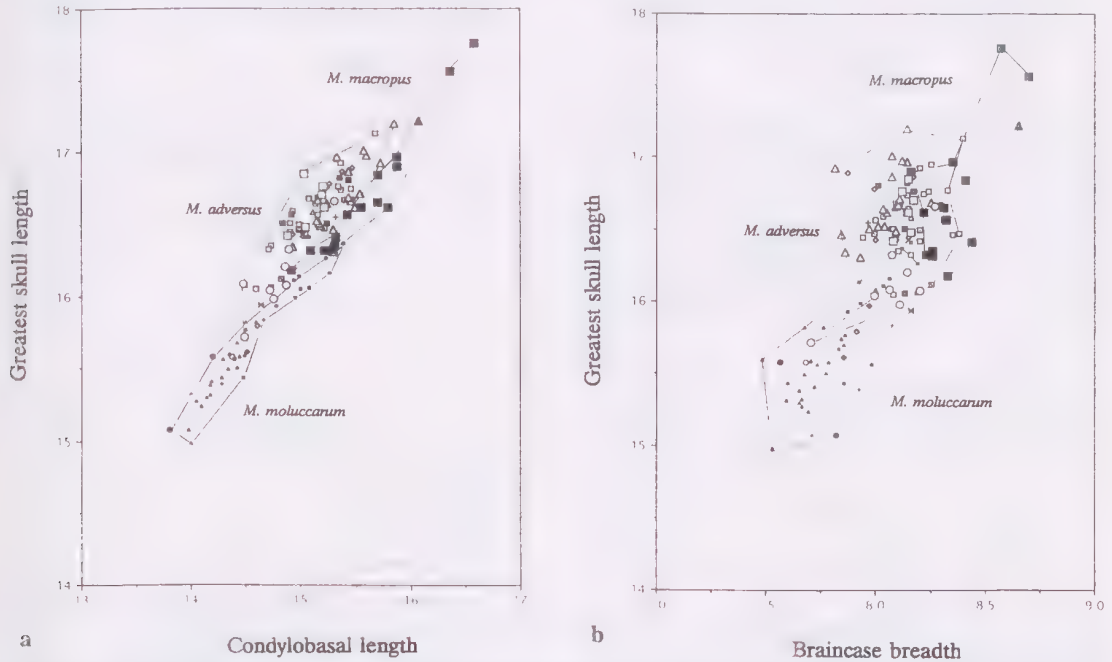


Figure 6 Plot of greatest skull length versus (a) condylobasal length and (b) braincase breadth, for male and female adult *Myotis adversus*, *M. moluccarum* and *M. macropus*. Locality codes as for Figure 2.

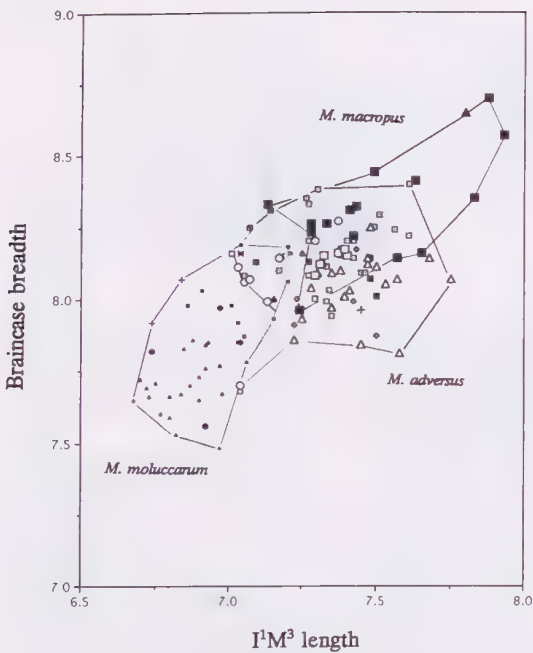


Figure 7 Plot of braincase breadth versus I¹M³ length for male and female adult *Myotis adversus*, *M. moluccarum* and *M. macropus*. Locality codes as for Figure 2.

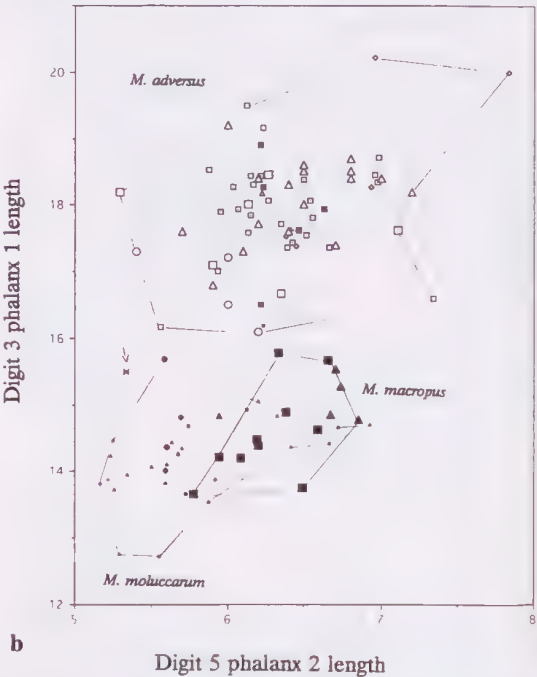
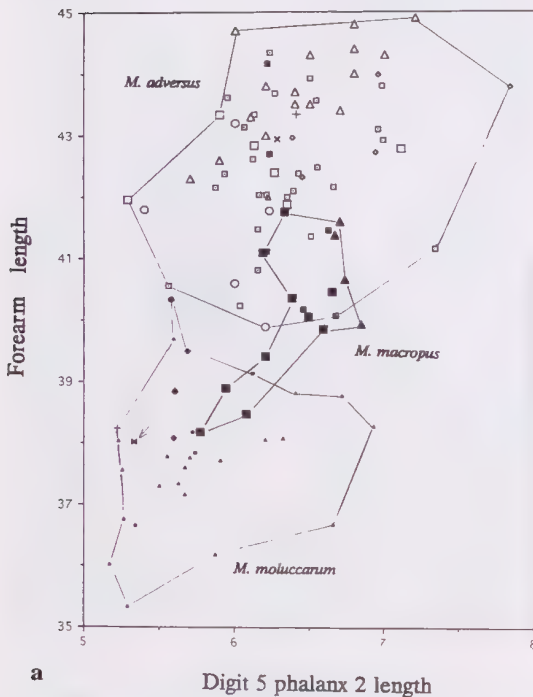


Figure 8 Plot of digit 5 phalanx 2 length versus (a) forearm length and (b) digit 3 phalanx 1 length for male and female adult *Myotis adversus*, *M. moluccarum* and *M. macropus*. Locality codes as for Figure 2.

large as that of I¹; I¹ posterior cusp two-thirds height of anterior cusp; I² labial cusp large, subequal in height to I¹ anterior cusp; I² lingual cusp well developed, much shorter than primary cusp, formed by oblique ventral projection of posterior lingual cingulum; I³ separate from C¹ by a diastema about equal in width to I³ breadth; I₁₋₃ not imbricate except for slight overlap between I₂ and I₃; I₁₋₂ tricuspid; I₃ much larger, its breadth (in tooth row) greater than that of I₁₋₂ – its breadth anteroposteriorly about twice that of I₁₋₂; I₃ occlusal surface subterete with four distinct cusps – a larger almost central crown – two smaller lateral (anterolateral one frequently irregular) crowns and a small lingual crown; C¹ lingual face concave, anterior face with groove traversing full length of tooth, posterior face with sharp ridge; C₁ with strong posterior and lingual cingula which frequently project to an anterior and posterior cingular cusplet; C₂ in close contact with I₃ and P₁; P¹ small, conical, suboval in occlusal view, less than half P⁴ height and *ca* one-quarter P⁴ size; P³ conical, minute, *ca* one-sixth P¹ size, in tooth row or partially intruded; P¹ and P⁴ cingulum not in contact; P₁ larger than P¹, *ca* four-fifth P₄ size; P₃ less than one-half P₁ height and *ca* one-third P₁ size, usually intruded from toothrow.

Colour

Dorsum Dark Grayish Brown, ventral surface a Blackish Neutral Gray tipped with Pale Neutral Gray. Patagia and ears Dark Grayish Brown.

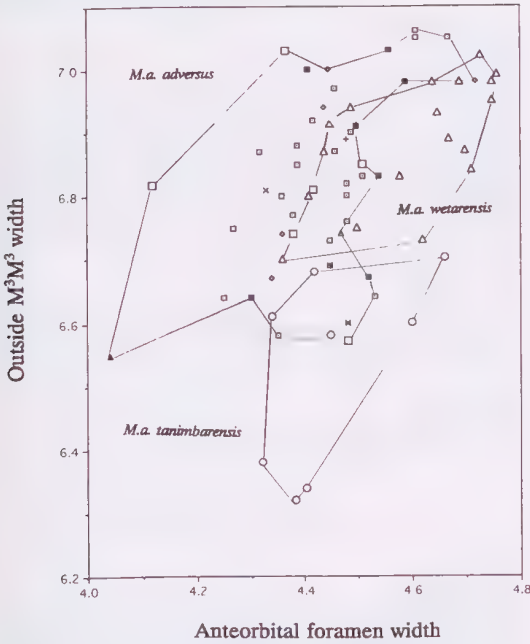


Figure 9 Plot of outside M³M³ width versus anteorbital foramen width for male and female adult *Myotis adversus adversus*, *M. a. tanimbarensis* subsp. nov. and *M. a. wetarensis* subsp. nov. Locality codes as for Figure 2.

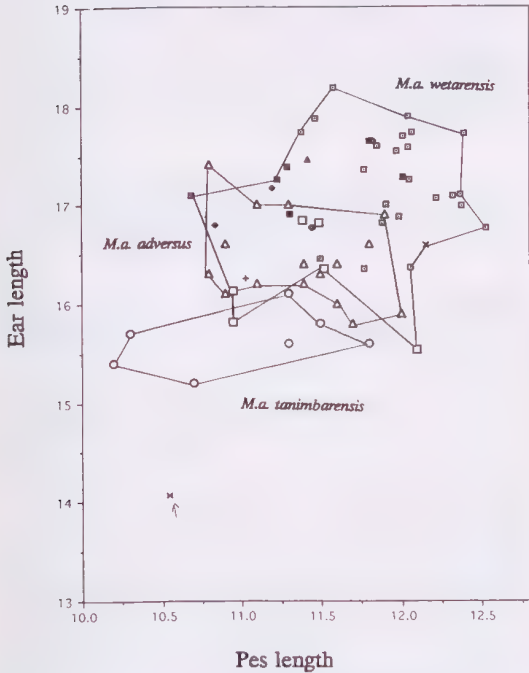


Figure 10 Plot of ear length versus pes length for male and female adult *Myotis a. adversus*, *M. a. tanimbarensis* subsp. nov. and *M. a. wetarensis* subsp. nov. Locality codes as for Figure 2.

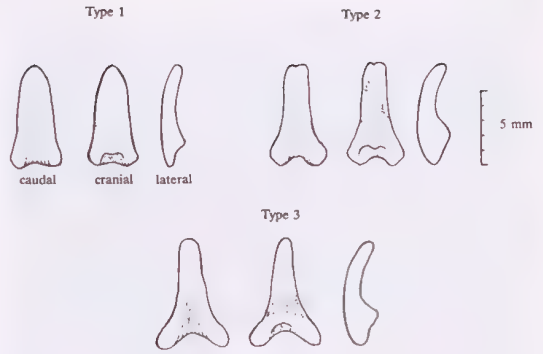


Figure 11 Baculum types: type 1 – *Myotis moluccarum* and *M. macropus*; types 2 and 3 – *M. adversus*.

Penis and baculum

Penis ca 3.5 long; glans penis a simple pear shape with ventral urethral slit. Baculum with base bifurcated to lesser or greater extent with distal end narrowing (types 1 or 2, Figure 11). Maximum length (mean, range, N) = 0.70 (0.60–0.83) 5.

Distribution

Peninsular Malaysia (?); Java; Kangean Island; Nusa Penida Island and Nusa Tenggara (Sumbawa Island; Moyo Island; Flores Island; Lembata Island; Pantar Island; Alor Island; Timor Island and Savu Island).

Myotis adversus tanimbarensis subsp. nov. Kitchener

Holotype

Museum Zoologicum Bogoriense (MZB) No. 15906; Western Australian Museum (WAM) field No. M43583; adult male, skull separate, carcase fixed in 10% formalin, preserved in 75% ethanol; liver stored at Western Australian Museum in ultrafreeze refrigerator; baculum separate; weight 9 gm; collected by D.J. Kitchener, R.A. How and I. Maryanto on 16 April 1993.

Type locality

7 km N. Saumlaki, Yamdena Island, Tanimbar Islands, Maluku Tenggara, Indonesia (7°54'00"S, 13°20'00"E); from large cave lit by large entrance, with deep well to sea.

Paratypes

Listed in 'Specimens Examined' section.

Diagnosis

Myotis adversus tanimbarensis differs from *Myotis adversus adversus* as detailed in the diagnosis of the latter subspecies.

It differs from *Myotis adversus wetarensis* in averaging smaller in all skull, dentary and dental measurements, except braincase breadth. For example, greatest skull length 16.14 (15.72–16.66) 8 v. 16.71 (16.34–17.20) 18; zygomatic width 10.07 (9.60–10.30) 3 v. 10.43 (10.21–10.62) 14; P³M³ length 7.34 (7.03–7.37) 8 v. 7.45 (7.22–7.75) 18; M³M³ width smaller relative to anteorbital breadth (Figure 9). It also differs in having all external measurements smaller. For example, ear length 15.6 (15.2–16.1) 7 v. 16.4 (15.8–17.4) 17; tibia length 18.5 (18.5–19.3) 7 v. 19.5 (18.7–20.6) 7; forearm length 41.2 (39.9–43.2) 7 v. 43.8 (42.3–45.2) 17; digit 5 metacarpal length 36.7 (35.1–39.3) 7 v. 39.6 (38.0–40.7) 17. Ear length shorter relative to pes length (Figure 10).

Description

The morphology of *M. a. tanimbarensis* is as described earlier for *M. a. adversus* except for differences noted in the earlier diagnosis and as follows: *M. a. tanimbarensis* has the skull at the junction of the parietal and frontal regions more inflated. The baculum of the holotype MZB 15906 was a type 3 (Figure 11) and had a greatest length of 0.71. The dorsal pelage Dusky Brown; ventral surface basal hairs Dusky Brown tipped with Pale Neutral Gray. Patagia and ears Dusky Brown.

Distribution

Known only from Yamdena Island, Tanimbar Group, Maluku Tenggara, Indonesia.

Etymology

Named after the Tanimbar Islands.

Myotis adversus wetarensis subsp. nov. Kitchener

Holotype

Museum Zoologicum Bogoriense (MZB) No. 15907; Western Australian Museum (WAM) field No. M44690; adult female, skull separate, carcass fixed in 10% formalin, preserved in 75% ethanol, weight 13.2 gm; collected by D.J. Kitchener and R.A. How on 23 September.

Type locality

2 km E. Ipokil, Wetar Island, Maluku Tenggara, Indonesia, (7°45'00"S, 128°48'20"E) from a large sunken cave.

Paratypes

Listed in 'Specimens Examined' section.

Diagnosis

Myotis adversus wetarensis differs from *Myotis adversus adversus* and *Myotis adversus tanimbarensis* as detailed in those earlier diagnoses.

Description

The morphology of *M. a. wetarensis* is as described earlier for *M. a. adversus* except for differences noted in the earlier diagnosis. The baculum of WAM 44706 is a type 3 (Figure 11) with maximum length 0.71. The dorsal pelage Dark Grayish Brown; ventral surface with basal hairs Dark Grayish Brown tipped with White; patagium Fuscous.

Distribution

Known only from Wetar Island, Maluku Tenggara, Indonesia.

Etymology

Named after Wetar Island.

Myotis adversus subsp. indet.

Remarks

The single adult male specimen from New South Wales (AM 13250) was classified by DFA to *Myotis adversus tanimbarensis*. While it is closest morphologically to that subspecies, it differs from it in having a skull with the cranium less inflated immediately posterior of the interorbital constriction; longer bulla 3.13 v. 2.96 (2.72–2.98) and generally smaller externally (see Table 1). For example, forearm length 38.0 v. 41.2 (39.9–43.2); ear length 14.1 v. 15.6 (15.2–16.1) 7 and tibia length 16.1 v. 18.5 (18.0–19.3) 7. It also has a baculum that is more broadly spatulate (type 1, Figure 11).

Myotis moluccarum (Thomas, 1915)

Leuconoe moluccarum Thomas, 1915: 170–172.

Diagnosis

Myotis moluccarum differs from *Myotis adversus* as detailed in the earlier diagnoses of the latter species.

It differs from *Myotis macropus* in averaging smaller for all skull, dentary and dental measurements. For example greatest skull length 15.64 (14.98–16.37) 37 v. 16.75 (16.18–17.76) 15; braincase breadth 7.81 (7.48–8.19) 37 v. 8.36 (8.14–8.70) 15; zygomatic width 10.06 (9.50–10.76) 34 v. 10.70 (10.20–11.42) 12; M³M³ width 6.41 (6.19–6.76) 37 v. 6.94 (6.64–7.37) 15; P³M³ length 6.92 (6.68–7.32) 37 v. 7.54 (7.13–7.93) 15. M³M³ width smaller relative to C¹C¹ width (Figure 12). It also averages smaller in all external measurements. For example, tibia length 16.7 (15.6–18.1) 37 v. 17.5 (16.5–18.3) 13; forearm length 38.2 (35.4–41.0) 37 v. 40.3 (38.2–41.8) 13; digit 3 metacarpal 37.2 (34.0–39.1) 37 v. 39.4 (37.2–41.1) 13. Forearm length generally longer relative to digit 5 phalanx 2 length (Figure 8a).

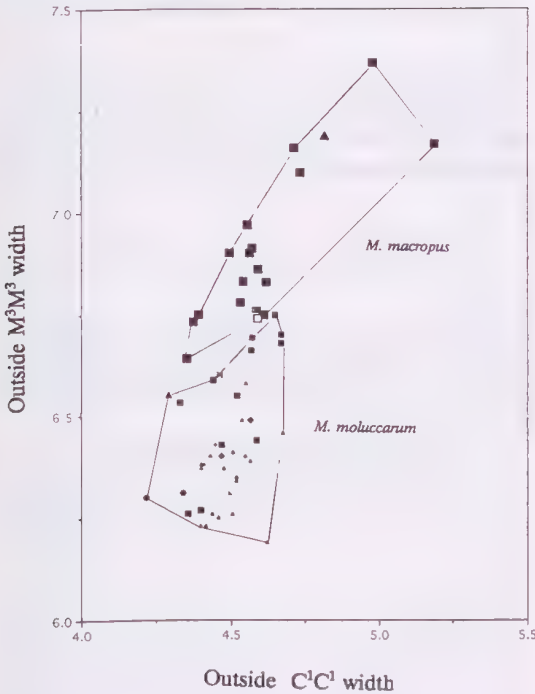


Figure 12 Plot of outer M^3M^3 width versus outer C^1C^1 width for *Myotis moluccarum* and *M. macropus*. Locality codes as for Figure 2.

***Myotis moluccarum moluccarum* (Thomas, 1915)**

Leuconoe moluccarum Thomas, 1915:

Holotype

British Museum No. 10.3.1.29 (original number 854); adult male; skin and skull separate; collected by W. Stalker in July 1909.

Type locality

Ara, Kei (= Kai) Islands, Maluku Tenggara, Indonesia.

Specimens examined

See 'Specimens Examined' section.

Diagnosis

[Our measurements of AM 23420 and SAM 21781, Solomon Is are followed, where available (in brackets) by the mean and range of the holotype measurements of *solomonis* from Troughton (1929) and five specimens listed in Phillips and Birney (1968)].

Myotis moluccarum moluccarum differs from *Myotis moluccarum richardsi* subsp. nov. in averaging smaller in all skull, dentary and dental measurements. For example, greatest skull length 15.48 (14.98–15.82) 22 v. 15.95 (15.39–16.37) 13; braincase breadth 7.70 (7.48–7.86) 22 v. 8.01 (7.85–

8.19) 13; zygomatic width 9.92 (9.50–10.28) 22 v. 10.32 (9.74–10.76) 13; I^1M^3 length 6.85 (6.68–7.06) 22 v. 7.03 (6.74–7.32) 13; braincase breadth narrower than C^1C^1 width (Figure 13). Ear generally longer relative to digit 5 metacarpal length (Figure 14).

It differs from the Solomon Island form of *Myotis moluccarum* in having both a larger anteorbital foramen width 4.16 (4.00–4.32) 22 v. 3.89–3.93 and C^1C^1 width 4.50 (4.40–4.68) 22 v. 4.22–4.34 [4.4(4.3–4.4)]. C^1C^1 width larger relative to braincase breadth (Figure 13). Forearm generally shorter 37.6 (35.4–39.7) 22 v. 38.8–40.4 [39.6 (38.5–41.3)] and a paler ventral pelage.

Description

The morphology of *M.m. moluccarum* is as described earlier for *M. a. adversus*, except for differences noted in the earlier diagnosis, and as follows: the median postpalatal spine projects further posteriorly, is broader, and projects less ventrally; mesopterygoid fossa broad with broad external ventral flanges on the pterygoid processes; such that the sphenorbital fissure is almost obscured from the ventral view; and the P^3 is usually well intruded from the tooth row such that P^1 and P^4 cingulum are often in contact.

Baculum with base slightly broadened and distal shaft spatulate (type 1, Figure 11), greatest length 0.71 (0.66–0.78) 3.

Dorsal pelage Burnt Umber; ventral surface basal

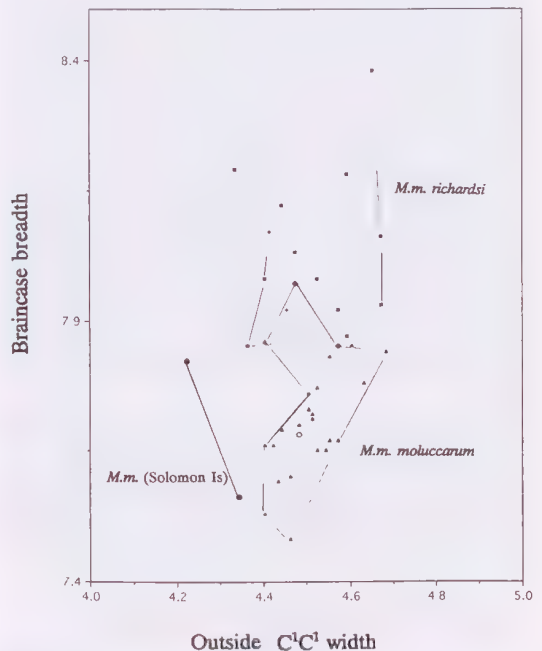


Figure 13 Plot of braincase breadth versus outer C^1C^1 width for *Myotis moluccarum moluccarum*, *M. moluccarum* (Solomon Is) and *M. m. richardsi* subsp. nov. Locality codes as for Figure 2.

hairs Dark Grayish Brown tipped with Pale Neutral Gray.

Distribution

Western Australia, Kai Islands, Seram, Papua New Guinea and probably Ambon.

Remarks

The earlier DFA indicated that on skull characters the two Papua New Guinea and the single Seram specimens allocated to the Western Australia *Myotis m. moluccarum*. However, on externals, one of these PNG specimens was intermediate between the Western Australian *M.m. moluccarum* and the Queensland/Northern Territory *M. m. richardsi*; the other PNG specimen allocated to this latter subspecies (there were no external measurements for the Seram specimen).

Direct comparison between the forms of *M. moluccarum* examined in this study with the holotype of this species from the Kai Islands was not possible.

Recent expeditions by us (Kitchener *et al.* 1993a) and by a team from the Australian Museum, also failed to collect *Myotis moluccarum* on the Kai Islands. Comparison of the Western Australian form with measurements of this holotype presented in Thomas (1915) indicated that it was clearly closer in size to this holotype than was the Queensland/Northern Territory form.

The form of *M. moluccarum* from the Solomon Is (*Anamygdon solomonis* Troughton, 1929) appears to be distinct from the other forms of this species. However, because we examined only two specimens we tentatively follow more recent classifications and retain this form in synonymy with *M. m. moluccarum*. It is noted that the P¹ and P⁴ cingulum of our two Solomon Island specimens were not in contact. In the holotype of *A. solomonis*, Troughton (1929: 91) stated that these two upper premolars were in contact. Their dorsal pelage was Dusky Brown; ventral pelage Burnt Umber with very slight frosting on tips; the venter was not 'pale' as in the other taxa reviewed herein. We did not observe the baculum of the Solomon Island form.

The subspecific taxonomy of *M. moluccarum* remains somewhat obscure, however its clarification will depend on availability for study of more extensive series of specimens from Maluku Tenggara, Papua New Guinea and the Solomon Is.

Myotis moluccarum richardsi subsp. nov.
Kitchener

Holotype

Queensland Museum (JM) No. 5335; adult female, skull separate, carcase preserved in 75%

ethanol; collected by P. Myroniuk on 22 December 1985.

Type locality

Gayundah Creek, Hinchinbrook Island, Queensland, Australia (18°22'S, 146°13'E); mist netted over creek in rainforest at sea level.

Paratypes

Listed in 'Specimens examined' section.

Diagnosis

Myotis moluccarum richardsi differs from *Myotis moluccarum moluccarum*, excluding the Solomon Island form, as detailed in the earlier diagnoses of that subspecies.

It differs from the Solomon Island form of *M. moluccarum* in the same way that it differs from *M. m. moluccarum* except that its ears are not notably shorter (see Figure 14 and Phillips and Birney 1968).

Description

The morphology of *M.m. richardsi* is as described earlier for *M.m. moluccarum* except for differences noted in the earlier diagnosis and as follows: P¹ and P⁴ cingulum occasionally in contact, but usually not. The baculum is also similar to *M.m. moluccarum* from Western Australia (type 1, Figure

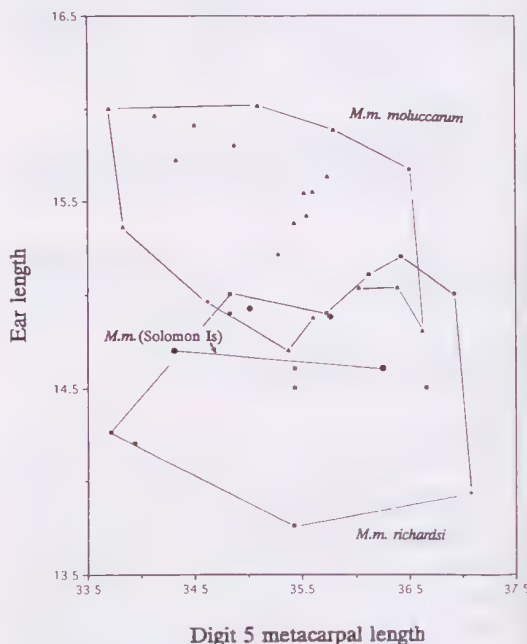


Figure 14 Plot of ear length versus digit 5 metacarpal length for *Myotis moluccarum moluccarum*, *M. moluccarum* (Solomon Is) and *M. m. richardsi* subsp. nov. Locality codes as for Figure 2.

11) – the one extracted had a greatest length of 0.73.

Pelage colour variable – dorsum ranges from Russet to Burnt Umber to Dark Grayish Brown. Ventral surface with basal hairs Cinnamon Brown or Dark Grayish Brown tipped with Pale Neutral Gray, or light Neutral Gray. Patagium and ears Russet or Fuscous.

Distribution

Queensland and Northern Territory, Australia.

Etymology

Named after Mr Greg Richards for his studies on the chiropteran fauna of Queensland.

Myotis macropus (Gould, 1855)

Vespertilio macropus Gould, 1855: un-numbered page of text.

Syntypes

Includes BMNH No. 53.10.22.32; skin (“alcoholic”), skull separate.

Type locality

South Australia

Specimens examined

See later section.

Diagnosis

Myotis macropus differs from *Myotis adversus* and *Myotis moluccarum* as detailed in the earlier diagnoses of these species.

Description

The morphology of *Myotis macropus* is as described earlier for *Myotis adversus*, except for differences noted in the earlier diagnosis. Also the baculum of the Victorian specimen (C25641) is long (0.81), broad and a spatulate type 1 form (Figure 11) rather than types 2 or 3 typical of *M. adversus*.

Distribution

South Australia and Victoria, Australia.

DISCUSSION

Myotis adversus (*sensu lato*) in the study region comprised three species and six subspecies. One specimen from New South Wales also appeared representative of *Myotis adversus* and is morphologically closest to *M. a. tanimbarensis*; it is not allocated to a subspecies.

It appears, then, that all three species in this species complex occur in Australia – *Myotis moluccarum* (northern Australia), *Myotis adversus* (New South Wales) and *Myotis macropus* (southeastern Australia).

Myotis adversus is widespread and appears to alter little in morphology from Java through Nusa Tenggara to Alor Island. This is indicated by the fact that the cluster of the large sample of specimens from Alor Island in discriminant function space incorporates all the other islands in Nusa Tenggara (Figure 3a,b). Wetar Island (Maluku Tenggara Administrative province), immediately to the east of Alor Island, is the first population of *Myotis adversus* in this island chain to noticeably diverge morphologically. This divergence was considerable, such that the Wetar individuals that misclassified to the Alor Group based on skull dentary and dental characters, comprised only two of 18 individuals, and based on external characters, only one of 16 individuals.

The Yamdena population (Kepulauan Tanimbar) further to the east again, and part of the outer Banda Arc of islands, also diverged further morphologically from the Alor Group of populations and also was quite distinct from the Wetar population. No individuals in the Yamdena population were misclassified to these other populations in the DFA. It is probably that this morphological divergence of the Wetar and Yamdena populations reflects their relative geographic isolation from other islands to the west. Alor Island, and many of the islands further to the west in the Inner Banda Arc, were either joined or separated by small water gaps during the last glacial maxima about 18,000 yrs BP, when the sea level fell by about 120 m. Wetar Island, however, is separated by a wide stretch of deep water of ca. 900 m depth (Indonesian Naval Hydrographic Survey maps, 1991) (Kitchener *et. al* 1990, Heaney 1991). Yamdena Island, in the Outer Banda Arc, is the most geographically isolated *M. adversus* population (except for the New South Wales specimen, if it is indeed *M. adversus*); further it has never been connected by dry land to these other island populations. However, distance of present day water gaps between populations, or closeness of past connection during the Pleistocene, are not the sole explanation for the morphological divergence of the Wetar and Tanimbar populations. This is because the Timor and Savu populations, which are also isolated geographically, both by relative wide current water gaps and by deep seas, do not appear to have similarly diverged morphologically. Perhaps the slightly drier climate of the Wetar and the wetter climate of Yamdena Islands compared to the islands to the west (Oldeman, 1980) has resulted in differential selection pressures on the morphology of the population of both Wetar and Yamdena Islands.

The distribution of *Myotis adversus* extends from Java along the island chain of the Lesser Sundas as far as Tanimbar only. *Myotis moluccarum* occurs on

the Kai Islands, Seram (and possibly to Peleng Island, Sulawesi and Irian Jaya – see Hill (1983: 160)), New Guinea, the Solomon Islands and northern Australia.

Hill (*loc. cit.*) notes that *M. a. carinatae* from Borneo and Sumatra is very similar to *M. moluccarum* but notes that “only limited material is available for comparison”. We have not examined that material.

The distribution of the *Myotis adversus* complex in eastern Indonesia presents a pattern of morphology somewhat different again from those recently reported for other bat species in that region. For example, the form of *Hipposideros diadema* from Java (*nobilis*) reaches Lombok Island, where it interfaces sharply across the sea strait of Sumbawa with the eastern form of *H. diadema* (*diadema*). *Rhinolophus simplex* and *Hipposideros sumbae*, Lesser Sunda endemic species, are widely distributed throughout the Inner Banda Arc but differentiate into identifiable morphological forms on the outer Banda Islands. The pteropodid *Pteropus lombocensis*, endemic to the Lesser Sunda Islands, has a distinct western form (Lombok and Sumbawa Is) and an eastern form which occurs as far east as Alor Island; this eastern form shows some further morphological variation. The pteropodid *Aethalops alecto* has a wide distribution on the mountain tops of Sumatra, Java, Bali and Lombok Islands. However, on these latter two islands it has differentiated morphologically, sufficient to warrant subspecific status (Kitchener and Maryanto 1993, Kitchener *et al.* 1992, 1993 a–d, 1995 a,b). Other studies, by us and our colleagues A. Suyanto and Maharadatunkamsi (unpublished data) on *Scotophilus kuhlii*, *Hipposideros ater*, *Rhinolophus affinis*, *Eonycteris spelaea* and *Macroglossus minimus*, also reveal a variety of distributional patterns of subspecies of chiroptera in Eastern Indonesia which no doubt reflect current geography, recent historic events and current climatic patterns in the region. Clearly, however, there is a complex interaction between all these factors which has resulted in this mosaic of intraspecific morphological differentiation.

SPECIMENS EXAMINED

Myotis adversus adversus

Java: Locality unknown, BMNH (401 405) (♂, ♀).

Kangean Island: Central region, 115°20'S, 6°55'E, MZB13349 (1♂)

Nusa Penida: Karangasari, 8°42'S, 115°35'E, WAM M (39627–839663, 39674, 39680, 39682) (2♂♂, 4♀♀).

Sumbawa Island: Desa Sangeang, 8°18'S, 118°56'E, WAM M (31541, 31546, 31554–5, 31567) (1♂, 4♀♀).

Moyo Island: Sebotok, 8°09'30"S, 117°37'15"E, WAM M 31907 (1♂).

Flores Island: Ratulodong, 8°11'00"S, 122°52'00"E, WAM M (32569, 32574, 32586) (3♂♂).

Lembata Island: Merdeka Hadakewa, 8°22'S, 123°31'E, WAM M 32358 (1♀).

Pantar Island: Batu Bakalang, 8°14'S, 124°18'E, WAM M 37742 (1♂).

Alor Island: Kalabahi, 8°14'S, 124°32'E, WAM M (37523–5, 37527, 37536, 37547, 37553, 37555, 37557, 37581, 37583–4, 37586–7, 37589–91, 37593, 37595–600) (8♂♂, 16♀♀).

Timor Island: Lifuleo Oisina, 10°18'S, 123°30'E, WAM M 38066 (1♂).

Savu Island: Menia, 10°29'S, 121°55'E, WAM M (35256–8, 35265) (1♂, 3♀♀).

Myotis adversus wetarensis subsp. nov. (all paratypes)

Wetar Island: Desa Ipokil, 7°50'S, 126°16'E, WAM M (44686–7, 44689–94, 44696, 44698–706) (1♂, 17♀♀).

Myotis adversus tanimbarensis subsp. nov. (all paratypes)

Yamdena Island: Saumlaki, 7°59'S, 131°22'E, WAM M (43581–5, 43589, 43618–9) (7♂♂, 1♀).

Myotis adversus subsp. indet.

New South Wales: Rocky Creek, 28°39'S, 153°20'E, AM M 13250 (1♂).

Myotis moluccarum moluccarum

Western Australia: Drysdale R. Nat. Park, 14°40'S, 127°00'E, WAM M (14063–5, 14067–77, 14079) (3♂♂, 12♀♀). Mitchell Plateau, 14°30'00"S, 125°47'20"E, WAM M (15763, 21571, 21582) (2♂♂, 1♀). Surveyors Pool, Mitchell Plateau, 14°40'20"S, 125°43'40"E, WAM M (21509–11) (2♂♂, 1♀). Prince Regent Reserve, 15°49'25"S, 125°37'03"E, WAM M 12255 (1♂).

Myotis moluccarum richardsi subsp. nov. (all paratypes)

Northern Territory: Melville Island, 11°18'S, 130°27'E, C 953 (sex unknown). Mungejirri Yaalput Waterhole, 14°32'S, 135°15'E, SAM M1810 (1♂).

Queensland: Brisbane, 27°28'S, 153°01'E, JM 2838, (1♀). Dowah Creek, JM (5000, 5003) (2♀♀). Hinchinbrook Island, 18°22'S, 146°15'E, JM 5335 (1♀). Jerona, Ayr, 19°34'S, 147°13'E, JM (7971–2, 7975) (1♂, 2♀♀). Lake Barrine, 17°16'S, 145°35'E, AM M 4901 (1♀). Macleods Creek, Cooktown, 15°26'S, 145°08'E, AM M 13317 (1♀). Noosa Heads,

26°25'S, 153°07'E, JM 9303 (1♂). Peach Creek, 13°41'S, 143°09'E, SAM M 16355 (1♂). Somerset Point, 10°45'S, 142°35'E, JM 5002 (1♀).

Seram Island: Locality unknown, BMNH 428 (1♀)

Papua New Guinea: Port Moresby, 9°27'S, 147°08'3, AM M 18824 (1♂).

Yuro, Central Province, 6°32'S, 144°51'E, AM M 15110 (1♂).

Myotis moluccarum (Solomon Islands)

Solomon Islands: Mbeu River. approx 6.5 km NW Tamaneke Village Marovo Lagoon, 8°18'S, 157°45'E, AM M 23420 (1♀). Pavora R. Choiseul Islands, 6°46'S, 156°32'E, AM M 21781 (1♀).

Myotis macropus

South Australia: Nildottie, 34°41'08"S, 139°36'36"E, SAM M (13373–6) (2♂♂, 2♀♀).

Victoria: Cloggs Cave, East Buchan, 37°30'S, 148°10'E, C (2986, 3568–70, 3684, 4352) (5♂♂, 1♀).

East Gippsland, (locality unknown) C25904, (♀). Glenelg River, 2 km W of Red Cap Creek, 38°01'S, 140°58'S, C26083 (1♂). Ovens River, 10.4 km NE of Mt Killawarra, 36°09'50"S, 146°13'40"E, C (25653, 25661) (1♂, 1♀). Rocky Creek, 50 km from confluence with Wingham River, 37°43'18"S, 149°29'24"E, C24908 (1♂). Scorpion Block, Nowa Nowa, 37°16'S, 147°58'E, C 26097 (1♀). Steep Bank Rivulet, 9.5 km NW of Wando Bridge, C 24870 (1♀). Goulburn River, 14.6 km SSW of Nathalia, 36°10'15"S, 145°06'40"E, C 25641 (1♂).

ACKNOWLEDGEMENTS

We are grateful for the support of Mr A. Reeves, Director, Western Australian Museum, Dr Soetikno, Director, Puslitbang Biologi, and Mr M. Amir, Director, Balitbang Zoologi, Bogor, Indonesia, and the Directors of Sub Balai Konservasi in Nusa Tenggara Barat (Ir. P. Supriadi), Nusa Tenggara Timur (Ir. J. Mochtar) and Maluku Tenggara (Ir. J. Rustandi).

A number of colleagues assisted in the field work of whom Dr R.A. How, Mr R.E. Johnstone, Western Australian Museum, and Mr Maharadatunkamsi and Mr A. Suyanto, Balitbang Zoologi, were principal. Mr C. Keast, Western Australian Museum, assisted in the preparation of skulls for this study. Mrs S. Dalton, Western Australian Museum, typed the manuscript.

The field work was supported by a number of grants, including National Geographic Society Research Grants, Washington and the Australian Nature Conservation Agency, Canberra. Freight costs were subsidised by Garuda Airlines.

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Manuscript received 19 May 1994; accepted 13 March 1995.

Morphological variation in Bearded Tomb Bats (*Taphozous*) in Maluku Tenggara and Nusa Tenggara Timur, Indonesia

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Abstract – Bearded Tomb Bats, *Taphozous melanopogon* and *T. achates*, were recently collected on Wetar, Tanimbar and Kai Islands, eastern Indonesia.

Morphological comparisons of skull, dentary, dental and external characters and a univariate and multivariate statistical analyses of 138 specimens, indicated that the animals from Wetar Island were *T. a. achates*. Those from the Tanimbar and Kai Islands were morphologically distinct from both *T. melanopogon* and *T. a. achates*, but were closer to the latter taxon. They are herein described as a new subspecies of *T. achates*, *T. achates minor*.

INTRODUCTION

An earlier study of the morphological variation of Bearded Tomb Bats in Nusa Tenggara, Indonesia, by Kitchener *et al.* (1993a) recognised the occurrence in that region of two species, *Taphozous m. melanopogon* Temminck, 1841 and *T. achates* Thomas, 1915. The former was found on islands in the Inner Banda Arc (Lombok, Sumbawa, Moyo and Alor), as well as Timor in the Outer Banda Arc. Koopman and Gordon (1992) also report that a specimen of *T. melanopogon* exists in the American Museum of Natural History from Kei (= Kai) Island. *Taphozous achates* occurred only on islands in the Outer Banda Arc (Savu, Roti and Semau and possibly also on Timor).

Kitchener *et al.* (1993a) noted that while there was little morphological differentiation in *T. m. melanopogon* among islands in Nusa Tenggara, there appeared to be some differentiation among populations of *T. achates*. These authors suggest that *T. m. melanopogon* is Laurasian in origin and may be a relatively recent inhabitant of Nusa Tenggara and speculate that “*T. achates* alone will be found to occur on the smaller Gondwanic islands such as Leti, Babar, Tanimbar, Kei (= Kai) and Aru”. The recent collection of Bearded Tomb Bats from Wetar, Tanimbar and Kai Islands by staff from the Western Australian Museum and Museum Zoologicum Bogoriense allows for this speculation to be examined.

Recent studies on morphological variation (and in some cases of genetic variation) have shown a tendency for some species of bats that are widely distributed in Nusa Tenggara and Maluku Tenggara to differentiate morphologically in the southeastern parts of these provinces, where the islands in the Inner and Outer Banda Arcs become

more isolated from the other islands in these areas (Kitchener and Maryanto 1993; Kitchener *et al.* 1993b; 1995a,b).

This paper will describe the morphological variation of the Bearded Tomb Bats from the southern region of Maluku Tenggara and report on the taxonomic status of these bats.

MATERIAL AND METHODS

Measurements from 111 adult specimens used in the previous analysis of morphological variation in *Taphozous* in this region presented in Kitchener *et al.* (1993a) were combined with measurements from an additional 33 adult specimens from Wetar Island (9), Kai Besar Island (12) and Selaru Island, Tanimbar Group (12) for statistical analysis. The measurements recorded were the same as those documented in that previous study. However, palate length in both this and the previous study was measured from the posterior margin of the palate to the posterior margin of the anterior palatal incisor, and not to the anterior edge of the C¹ alveoli as figured in Kitchener *et al.* (1993a: figure 1).

The measurements were as follows: GSL, greatest skull length; IOW, least interorbital breadth; POW, postorbital breadth; CW, cranial breadth; MW, mastoid width; ZW, zygomatic width; PPL, post palatal length; PL, palatal length; DBC, distance between cochleae; BL, bulla length; GBPL, greatest basal pit length; DL, dentary length; C¹BW, C¹ basal breadth; C¹C¹B, width across C¹C¹ labial surfaces at alveoli; M³M³B, width across M³M³ labial surfaces at alveoli; C¹M³L, maxillary tooth row length, from C¹alveoli anterior edge to M³ alveoli posterior edge; M²L, M² crown length; M²W,

larger set of characters. This reduced set of characters was selected because the sample size of the smallest island group was less than the total number of characters considered. This reduced set of characters was selected because they provide values that minimise Wilk's Lambda. All analyses used the statistical package SPSS PC+.

Univariate Statistics

The mean, standard deviation, and range of measurements of skull, dentary and dental characters of both adult male and adult female *Taphozous* from Wetar, Tanimbar and Kai Island are presented in Table 1. Comparable measurements for specimens from other islands in Nusa Tenggara are presented in Kitchener *et al.* (1993a: table 2). These measurements indicate that the Tanimbar and Kai individuals were of similar size but the Wetar individuals were generally larger in skull, dentary and dental measurements.

Multiple regression analysis

Skull, dentary and dental characters

This analysis examined the association between the main effects of sex, age and island and the recorded measurements and the interactions between these effects.

Sex and age

There were no significant interactions between these effects and no significant association between these measurements and age and sex, except for M² width and age ($F_{2,82}=5.821$; $p=0.004$).

Island

All characters were significantly associated with

island at $P < 0.001$, except for postorbital width ($P = 0.013$).

Externals

Sex and age

There were no significant associations between sex and age and the external characters. There was, however a significant interaction for tail to vent length between sex and island ($F_{6,88}=3.863$; $P=0.002$).

Island

Only snout to vent length, greatest tragus breadth, digit 4 metacarpal length, digit 5 metacarpal length and pes length were not significantly associated with island; tail to vent length was the most significantly associated variable ($F_{6,88}=10.699$; $P<0.001$).

Discriminant function analysis (DFA)

Skull, dentary and dental characters

Because of the absence of significant sexual dimorphism and the significant association of only one character (M^2 width) with age, the DFA based on skull, dentary and dental characters and the 11 island populations (Lombok, Sumbawa, Moyo, Alor, Wetar, Savu, Roti, Semau, Timor, Tanimbar and Kai Besar) was run for males and females combined, and all characters (17), except M^2 width.

A DFA run with a reduced set of five characters (dentary length, greatest basial pit length, bulla length, M² length and interorbital breadth) and three island groups [the Lombok Group (Lombok, Sumbawa, Moyo, Alor and Timor); the Savu Group (Savu, Roti, Semau and Wetar); and the Tanimbar

Table 1 (continued)

[illegible]

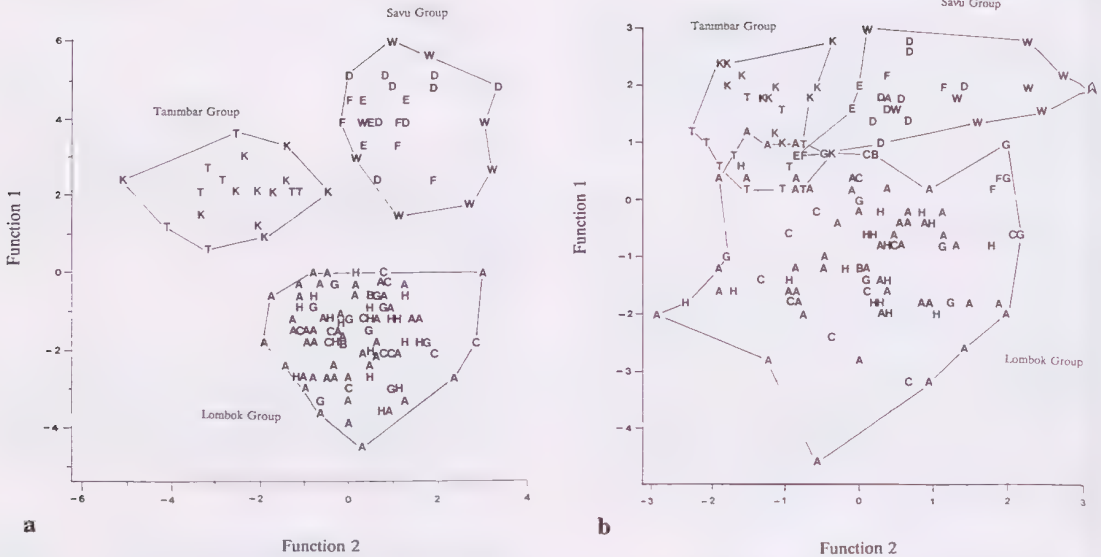


Figure 2 Canonical variate analysis for both adult male and adult female Bearded Tomb Bats based three island groups (Tanimbar Group; Savu Group, and Lombok Group). The plots of Functions 1 and 2 were based on (a) five selected skull, dentary and dental characters and (b) five selected external characters. The island codes within these three groups were as follows: A, Lombok; B, Alor; C, Timor; D, Roti; E, Savu; F, Sema; G, Moyo; H, Sumbawa; W, Wetar; K, Kai and T, Tanimbar.

Group (Yamdena and Kai Besar)] produced a similar association of these island populations in Discriminant Function space to that produced by the above DFA using all islands and 17 characters. This latter DFA produced two significant Functions (Figure 2a). Function 1 explained 82.5% of the variance and Function 2, 17.5%. All individuals were correctly classified to their appropriate island population.

The Lombok Group separated from both the Savu and Tanimbar Groups on Function 1. The characters loading heavily (>0.5) on Function 1 were dentary length and greatest basal pit length (Table 2a). The Tanimbar Group separated from the Savu Group and partially from the Lombok Group on Function 2. The characters loading heavily (>0.5) on Function 2 were greatest basal pit length and M^2 length (Table 2).

External characters

All external characters, except snout to vent length (which showed an interaction between sex and island), were included in a DFA of these characters based on the same three groups identified above (Lombok, Savu, and Tanimbar). This DFA was also run using a reduced set of five characters (tibia length, digit 3 metacarpal length, digit 3 phalanx 1 length, digit 5 metacarpal length and ear length) and it this latter DFA that is presented here. The DFA extracted two very significant Functions. Function 1, which explained

75.5% of the variance, separated both the Savu and Tanimbar Groups from the Lombok Group (Figure 2b). The character that loaded heavily (>0.5) on Function 1 was tibia length (Table 2b). Function 2, which explained 24.5% of the variance, separated the Savu and Tanimbar Groups. The character loading heavily (>0.05) on Function 2 was digit 3 metacarpal length (Table 2b). A total of 87.9% of individuals were classified to their correct island group. Misclassifications were as follows: Two Savu Group animals to the Tanimbar Group; five Lombok Group animals to the Savu Group and 10 Lombok Group animals to the Tanimbar Group.

The Lombok, Savu and Tanimbar Groups were clearly separated in Discriminant Function space based on skull, dentary and dental characters, but less clearly so on external characters. Further, it is apparent from these plots that within these Groups there is little morphological differentiation between the islands. This is indicated by the observation that the Lombok Group cluster is defined in DF space by individuals from a single island (Lombok) and similarly the Savu Group is defined by Wetar individuals. The Yamdena and Kai Besar specimens also overlap considerably (Figure 2). In the previous study by Kitchener *et al.* (1993a) the Lombok Group represent *Taphozous m. melanopogon* and the Savu Group *T. achates*. Consequently the Wetar Island individuals classify as *T. achates*. The Tanimbar Group individuals are morphologically distinct from both these above taxa. However, the

Table 2 Standardised and unstandardised (in brackets) Canonical Variate Function coefficients for three island groupings (the Lombok, Savu and Tanimbar groups – see text) using a reduced set of five (a) skull, dentary and dental characters and (b) external characters.

Character	Function 1	Function 2
Dentary length	0.9925 (3.9673)	−0.0351 (−0.1404)
Basial pit length	−0.6740 (−5.1426)	0.5109 (3.8982)
Bulla length	0.4514 (−3.5766)	0.4798 (3.8009)
M ² length	0.1256 (2.0740)	0.6495 (10.7288)
Interorbital breadth	0.3673 (1.9550)	−0.1179 (−0.6275)
Constant	−42.9653	−50.0386
Variance explained (%)	82.5	17.5

Table 2a

Character	Function 1	Function 2
Tibia length	0.8558 (0.8429)	0.1265 (0.1246)
Digit 3 metacarpal length	−0.2202 (−0.1719)	0.7704 (0.6014)
Ear length	0.4127 (0.3279)	0.2918 (0.2318)
Digit 3 phalanx 1 length	−0.4681 (−0.6943)	−0.0529 (−0.0785)
Digit 5 metacarpal length	−0.1177 (−0.0836)	0.3315 (0.2496)
Constant	0.4272	−48.8648
Variance explained (%)	75.5	24.5

DFA of all 11 islands and all skull, dentary and dental characters indicate that on Function 3 individuals from the Savu and Tanimbar Groups overlap considerably (graph not presented) indicating that individuals from the Tanimbar Group were associated in DF space with *T. achates* rather than with *T. m. melanopogon*. In the following section the populations from Tanimbar and Kai Islands are described as a new subspecies of *T. achates*.

TAXONOMY

Taphozous achates minor subsp. nov. Kitchener

Holotype

Museum Zoologicum Bogoriense (MZB) No. 15908 (field number M42899), adult male, carcase fixed in 10% formalin and preserved in 70% ethanol, skull removed, cleaned and separate, liver stored in ultrafreeze at the Western Australian Museum.

Type locality

Pulau Kelapa, 2 km W Elat, Kai Besar Island

Kepulauan Kai (05°39'S, 132°59'E), mist netted from the mouth of an open well-lit cave on the beach, by D.J. Kitchener and R.A. How on 19 October 1992.

Paratypes

Yamdena Island, Kepulauan Tanimbar Desa Olilit, 1 km S Saumlaki (from a World War II Japanese made tunnel) (7°59'S, 131°22'E), 2 ♂ 9 ♀, WAM M (43527, 43529–31, 43538, 43541–43, 43547–49). 2 km S Desa Lat Dalam, (from a large 'doline' cave, among a number of other limestone caves) (7°03'S, 131°07'E), 1 ♂, WAM M 43672.

Kai Besar Island, Kepulauan Kai, beach cave, Pulau (= islet) Kelapa, 2 km W Elat, Kai Besar Island (05°39'S, 132°59'E), 4 ♂ 8 ♀ ♀, WAM M (42886–88, 42890–91, 42893–94, 42896–97, 42899–900, 42902).

Diagnosis

Taphozous achates minor differs from *T. a. achates* in averaging smaller in all characters measured (Table 1 and Kitchener *et al.* 1993: table 2)). For example, greatest skull length 20.55 (19.94–21.12) 24 v. 21.54 (20.91–22.55) 28; interorbital breadth 6.23 (5.82–6.62) 24 v. 6.48 (5.95–6.95) 28; zygomatic width 12.87 (12.42–13.19) 24 v. 13.22 (12.88–13.78) 26; bulla length 4.73 (4.57–4.86) 20 v. 4.97 (4.75–5.55) 27; greatest basial pit length 3.78 (3.49–4.07) 24 v. 4.04 (3.85–4.34) 28; C'M³ (alveoli) length 8.77 (8.45–9.12) 24 v. 9.23 (8.85–9.74) 28; M² (crown) length 1.96 (1.79–2.06) 24 v. 2.15 (2.07–2.28) 28; tail to vent length 26.7 (23.8–30.8) 24 v. 27.3 (23.4–31.6) 28; radius length 61.8 (59.5–64.1) 24 v. 63.8 (61.1–65.4) 28; tibia length 24.5 (23.8–25.3) 24 v. 25.5 (23.3–26.8) 28. Also M² crown length and bulla length shorter relative to least interorbital breadth (Figure 3a,b); dentary length generally shorter relative to greatest basial pit length (Figure 4); and digit 3 metacarpal length shorter relative to tibia length (Figure 5).

It differs from *Taphozous m. melanopogon* from these southern Indonesian islands by having mature adult males with a pale brown rather than a black throat beard. Most skull, dentary and dental characters average smaller. For example cranial breadth 9.63 (9.42–9.80) 24 v. 9.78 (9.46–10.22) 92; distance between cochleae 2.13 (2.01–2.41) 24 v. 2.27 (1.89–2.66) 92; bulla length 4.73 (4.57–4.86) 20 v. 4.97 (4.59–5.42) 91; greatest basial pit length 3.78 (3.49–4.07) 24 v. 4.09 (3.73–4.36) 92; radius length 61.8 (59.5–64.1) 24 v. 63.4 (60.9–66.1) 90. Some characters average larger. For example, least interorbital breadth 6.23 (5.82–6.62) 24 v. 5.99 (5.60–6.33) 92; zygomatic width 12.87 (12.42–13.19) 24 v. 12.60 (11.98–13.16) 92; tail to vent length 26.7 (23.8–30.8) 24 v. 24.6 (18.8–29.5) 90; and tibia length 24.5 (23.8–25.3) 24 v. 23.3 (19.9–25.5) 90. Least interorbital breadth greater relative to M² length

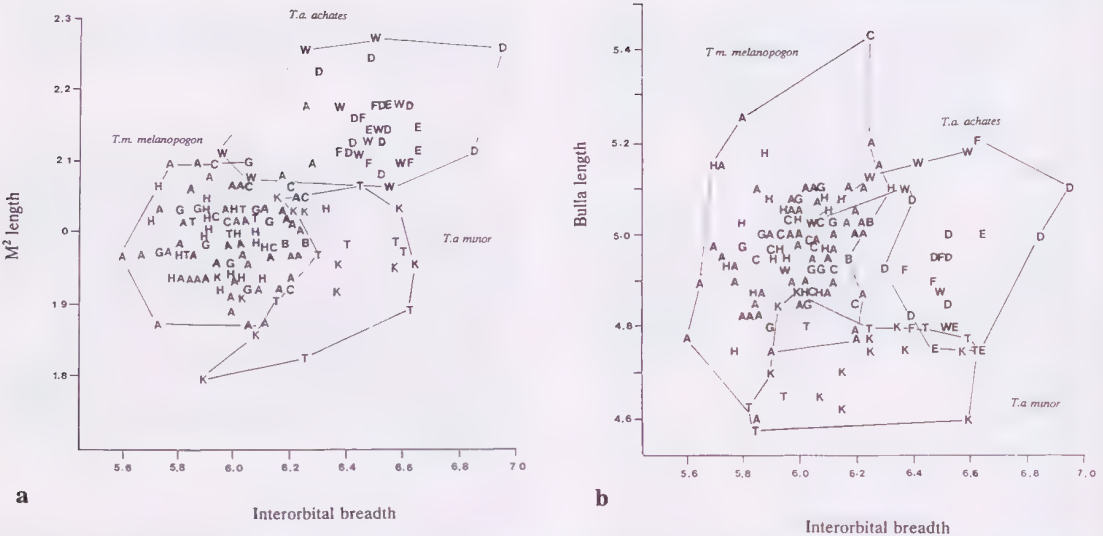


Figure 3 Plots of least interorbital breadth versus (a) M^2 length and (b) bulla length for both adult male and adult female *T. m. melanopogon*, *T. a. aches* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

and bulla length (Figure 3a,b); greatest basal pit length shorter relative to dentary length (Figure 4) and tibia length generally longer relative to digit 3 metacarpal length (Figure 5).

Description

Apart from the differences mentioned in the above diagnoses *T. a. minor* is very similar morphologically and in its pelage colour to *T. a. aches*.

Distribution

Known only from Yamdena Island and Kai Besar, Maluku Tenggara, eastern Indonesia.

Etymology

The name *minor* is from the latin referring to the small size of the Yamdena and Kai Besar form of *T. aches* compared to members of the nominate subspecies.

DISCUSSION

The Bearded Tomb Bats from Tanimbar and Kai Islands are most similar to *T. a. aches* but differ in being generally smaller in most characters; some skull and external characters also differ in shape. For example, M^2 crown length, bulla length and digit 3 metacarpal length. Specimens from Wetar Island were *T. a. aches* and were not differentiated morphologically from the other known populations of this nominate subspecies on Semau, Roti, and Savu Islands. In fact these latter

populations of *T. a. aches* were included within the Wetar Island population cluster in discriminant function space. This suggests that the Rotinese population had not noticeably differentiated from the nominate subspecies as suggested by Kitchener *et al.* (1993a).

Interestingly, *T. aches* occurred on Tanimbar

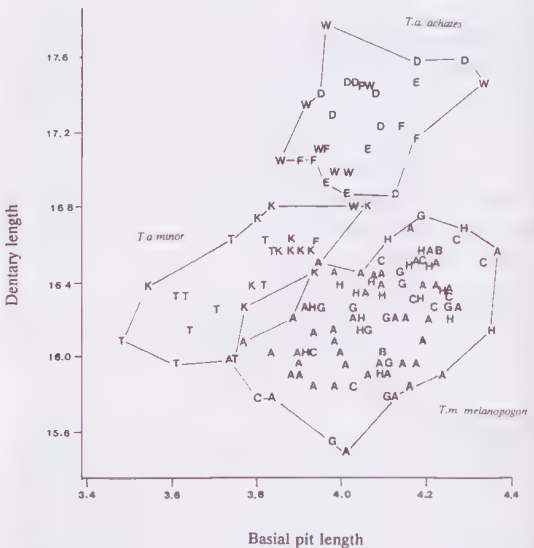


Figure 4 Plots of dentary length versus greatest basal pit length for both adult male and adult female *T. m. melanopogon*, *T. a. aches* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

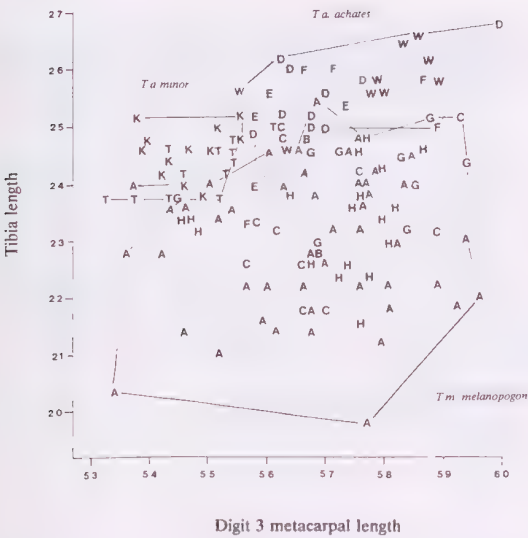


Figure 5 Plot of tibia length *versus* digit 3 metacarpal length for both adult male and adult female *T. m. melanopogon*, *T. a. aches* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

and Kai Islands as predicted by Kitchener *et al.* (1993a). Its distribution on the islands to the immediate south and north of Timor islands add credence to its presumed presence also on Timor Island (see Kitchener *et al.* 1993a). We have not examined the specimen from Kai Island which Koopman and Gordon (1992) attributed to *T. melanopogon*, but consider that it most probably also represents *T. aches minor*.

The morphological differentiation of *T. aches* on the eastern islands of Kai and Tanimbar reflects a pattern of intraspecific differentiation observed in other mammal species in the region. For example, *Hipposideros sumbae*, *Pteropus lombocensis* and *Cynopterus nusatenggara*, all Nusa Tenggara endemics, differentiate morphologically into western and eastern forms (Kitchener and Maryanto 1993, Kitchener *et al.* 1995c,d). The bats *Hipposideros diadema*, *Nyctimene albiventer*, *N. cephalotes*, *Syconycteris australis*, *Myotis adversus*, *Rhinolophus affinis* and *R. simplex*, all species with more widespread distributions, also differentiate morphologically within this region (Kitchener *et al.* 1992, Kitchener *et al.* 1993; Kitchener *et al.*; in press 1995a–d; Maharadatunkamsi 1990). This differentiation becomes more extreme on the more remote eastern islands of the Inner Arc, or on the islands of the Outer Banda Arc that have been continuously isolated by seas from other island populations. Interestingly, the House Mouse, *Mus musculus castaneus*, which is widely distributed

throughout Indonesia, also differentiates into a distinct form on Wetar and Kisar Islands (Kitchener, unpublished data).

Other specimens examined

Taphozous aches aches
Desa Ipokil, Wetar Island, Nusa Tenggara Timur (7°50'S, 126°16'E), 4 ♂♂ 5 ♀♀ WAM M(44510, 44520–27).

ACKNOWLEDGEMENTS

We are grateful for the support of Mr A. Reeves, Director, Western Australian Museum and to Dr Soetikno, Director, Puslitbang Biologi, and Mr M. Amir, Director, Balitbang Zoologi, Bogor Indonesia and the Directors of Sub Balai Konservasi in Nusa Tenggara Barat (Ir. P. Supriadi), Nusa Tenggara Timur (Ir. J. Mochtar) and Maluku Tenggara (Ir. J. Rustandi).

A number of colleagues assisted in the field work of whom Dr R.A. How, Mr R.E. Johnstone, Western Australian Museum, and Ir. Maharadatunkamsi and Ir. I. Maryanto, Balitbang Zoologi, were principal. Mr C. Keast, Western Australian Museum, assisted in the preparation of skulls for this study. Mrs S. Dalton, Western Australian Museum, typed the manuscript.

The field work was supported by a number of grants, including National Geographic Society Research Grants, Washington and the Australian Nature Conservation Agency, Canberra. Freight costs were subsidised by Garuda Airlines.

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Manuscript received 25 May 1994; accepted 13 February 1995.

A new tegastid (Tegastidae: Harpacticoida: Copepoda) from southwestern Australia: *Syngastes dentipes* sp. nov.

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Abstract – In coastal waters of Western Australia, the harpacticoid family Tegastidae is represented by about two dozen species, belonging to the genera *Syngastes*, *Tegastes* and *Parategastes*. A new species, *Syngastes dentipes*, is described. The species is characterized by the enlarged maxilliped with prominent teeth on its claw.

INTRODUCTION

In the littoral meiobenthos, copepods generally are second to nematodes in abundance, and in habitats rich in coarse interstitia, they may be the most numerically important taxon. Most meiobenthic copepods are harpacticoids. Recent studies on shallow water meiobenthos at Rottnest Island, Western Australia, revealed a remarkably rich fauna. Harpacticoids were represented with a diversity of body forms which reflect a wide range of adaptations to ecological niches. The majority of species were more or less pyriform or cylindrical, with or without conspicuous spines. Others, such as the dorsoventrally flattened Porcellidiidae, were very abundant on and amongst algae on exposed or semi-exposed shore-lines, whereas the laterally compressed, amphipod-shaped Tegastidae, also members of the phytal fauna, were found in less exposed areas, generally associated with habitats rich in microcavernes.

From southern Australia, a single tegastid species (*Tegastes* sp.) was mentioned by Nicholls (1941) half a century ago. Shallow water samples, taken recently around Rottnest Island, proved the existence of almost two dozen tegastid species, with representatives of the genera *Syngastes*, *Tegastes* and *Parategastes*. Four species have been described recently (Bartsch 1993, 1994), and emendations and descriptions of other species are in preparation.

MATERIAL AND METHODS

The specimens described were collected in January 1991 off Rottnest Island, Western Australia, from a substratum including algal holdfasts, sponges and other colonial organisms at a depth of 7–10 m. Animals were extracted by washing over a 100 µm sieve. The meiofauna was preserved in ethanol.

Measurements of whole specimens were made in lactic acid. Dissected specimens were mounted in glycerine jelly. The figures were drawn using a camera lucida. The decimal system gives position of a seta, or other structure, with reference from proximal to distal end of a segment. The setal formula shows number of inner setae on the basal segment : inner setae on succeeding segment : inner, apical and outer setae on distal segment : outer setae on preceding segment : outer setae on basal segment. Filaments and denticles mean seta-like or scale-like structures not arising from a pore.

Abbreviations used in text and figures: Ae, aesthetasc; A1, first antenna (antennule); A2, second antenna; c, cavity; ca, cylindrical appendage; dd, denticles; enp, endopod; ep, epicuticular droplets; exp, exopod; lr, lamellar ridges; Md, mandible; mp, median process; mt, median tine; Mx1, first maxilla (maxillula); Mx2, second maxilla; Mxp, maxilliped; p, pore(s); pp, porosity; ps, pore from seta; pvc, posteroventral corner; P1 to P5, first to fifth leg; s, seta; sP5, setae of P5; ss, setulae; ta, tongue-like appendage.

The holotype is deposited in the Western Australian Museum, Perth (WAM), and paratypes in the WAM and the author's collection.

SYSTEMATICS

Family Syngastidae

Genus *Syngastes* Monard

Syngastes dentipes sp. nov.

Figures 1–30

Material Examined

Holotype

♀, Duck Rock off Rottnest Island, Western Australia, Australia (31°59'S, 115°32'E), sample

with algal holdfasts and sponges, sand, 7–10 m depth, 9 January 1991, coll. P.A. Hutchings (WAM 17–95).

Paratypes

Australia: Western Australia: 1 ♂ (WAM 18–95); 1 ♂ (WAM 19–95); 2 ♀, 2 ♂ (author's collection); all from type locality and date.

Diagnosis

Female 530–560 µm, male 427–458 µm. Integument uniformly and delicately punctate. Female and male with four and three free thoracic somites respectively. Female A1 five-segmented, male A1 seven-segmented. Mx2 slender, its basis seven times longer than wide. Maxillipedal endopod widened; basal appendage cylindrical, heavily sclerotised; tongue-like appendage slender. Maxillipedal claw with two rows of conspicuous teeth. P1-exp slightly smaller than endopod. P4-enp with a single seta. Female P5 with baseopod and exopod almost completely fused. Male P5 undivided.

Description

Female

Length 530 (holotype, Figure 1) to 560 µm, height 360 (holotype) to 365 µm. Colour of ethanol-preserved specimens light-brown. Integument of most of cephalothorax, as well as that of posterior somites, delicately punctate; in a 20–25 µm wide ventral portion fine punctation of cephalosome replaced by epicuticular droplets (Figure 2), which are arranged like beads on a string. Integument of lateral flanks of genital somite delicately reticulate rather than punctate. All somites with pores (Figure 1); pores generally opening at outer surface of somites; row of four ventralmost pores on cephalosome opening at inner flank of cephalosomal shield.

Cephalothorax 295 µm long. Ventral margin of cephalosome with about eight 4–5 µm long setulae; each setula with 10–15 µm long canalculus penetrating the tegument. Similar setulae present also on cephalic shield and on posterior somites. Cephalothorax with two pairs of setae, one lateral, the other dorsal. Cephalothorax with internal sclerite extending dorsally for 90 µm. Succeeding four free thoracic somites 65, 90, 127, and 68 µm long. Third somite almost twice length of second and fourth free somite. First to third somite with one, two, and two setae, respectively. Delicate setulae, similar to those present along ventral margin of cephalosome, inserted 10–20 µm removed from ventral margin of epimera. Genital somite 74 µm long. Enlarged egg-reservoir with posteriormost edge extending slightly beyond anal

cone; ventral edge truncate. Postgenital somites small, not fused with genital somite.

A1 (Figure 3) five-segmented; segments 55, 57, 38, 22, and 30 µm long. Number of setae: 1, 11, 9, 4 + Ae, 16 + Ae. Seta on A1–1 as long as segment 1. Aesthetasc on A1–4 90 µm (holotype) to 110 µm long, and 4 µm wide, that on A1–5 50 µm long, 1–2 µm wide.

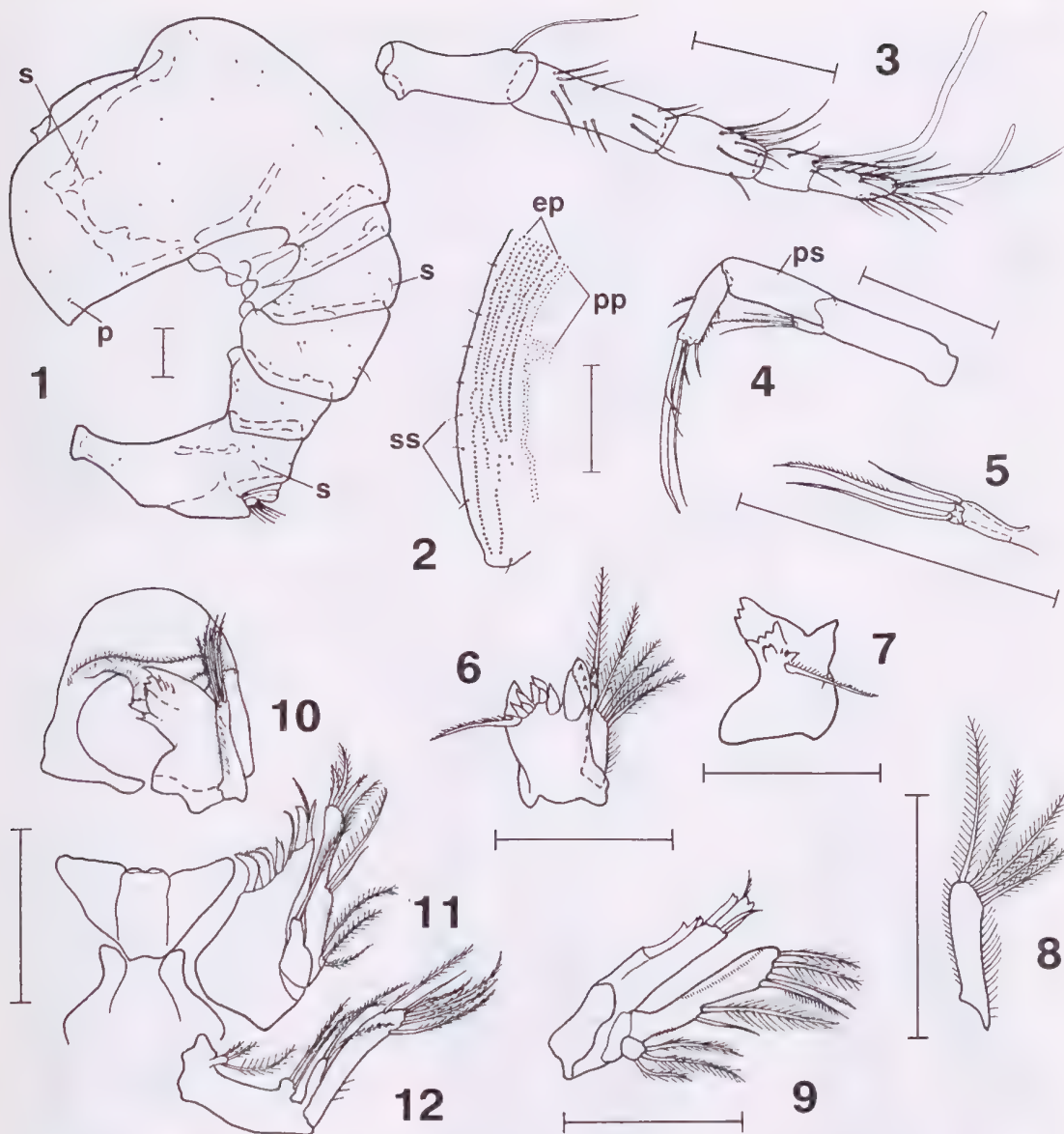
Exopod (Figures 4, 5) of A2 small, two-segmented; 11 µm long basal segment with one seta; 2 µm long apical segment with two setae, both longer than exopod, one of the setae distinctly serrate. Basal and apical segment of endopod 40 and 30 µm long. Basal segment with row of delicate filaments along posterior (ventral) margin, and a pore, but no seta, on anterior (dorsal) margin at 0.55 relative to length of segment. Apical segment posteriorly with three contiguous clusters of filaments, and anteriorly with two slightly plumose setae at 0.4 and 0.6 respectively. With six apical setae, two of which are claw-like, 25 and 60 µm long; remaining setae slender.

Mandibular gnathobase (Figures 6, 7, 10) with stout, serrate and two to three crowned teeth, and a long seta. Palp (Figure 8) undivided, flattened and ending with five bilaterally plumose setae. Edges of palp lined with filaments.

Mx1 as in male (Figure 11) with wide, flattened arthrite armed with five wide, apically serrate spines and three setae. Seta of coxa bearing two rows of filaments and extending to apex of basis. Flattened basis (Figure 9) with row of delicate filaments; four terminal setae with filaments. Two endopodal setae present, the longer one almost twice as long as the other seta and lined with filaments. Exopod with three setae, one of which is short, the two other subequal in length; all three setae with bilateral filaments.

Mx2 as in male (Figure 12) with two slender segments. Basal segment (syncoxa) 44 µm long and 12 µm wide, its posterior margin bare. Basal endite with three, middle endite with two plumose setae. Two setae on distal endite 2.0 and 2.5 times longer than endite and bearing filaments. Basis of Mx2 very slender, 42 µm long and 6 µm wide, with scattered, delicate filaments. Basis ending with setiform claw and five plumose setae.

Maxilliped subchelate, inserted on small pedestal. Maxillipedal basis (Figure 13) slender, 130 µm long. Surface of segment smooth. No filaments around medial fovea (fovea from tendon). Endopodal segment widened (Figures 14, 15); with median tooth-like projection, flattened median tine, four small lateral denticles (Figure 14), and about 35 medial denticles (Figure 15). Heavily sclerotised cylindrical appendage with spinose apex and short setula-like aesthetasc. Stalked, tongue-like appendage slender, with spinose edge and short setula. Maxillipedal claw as long as



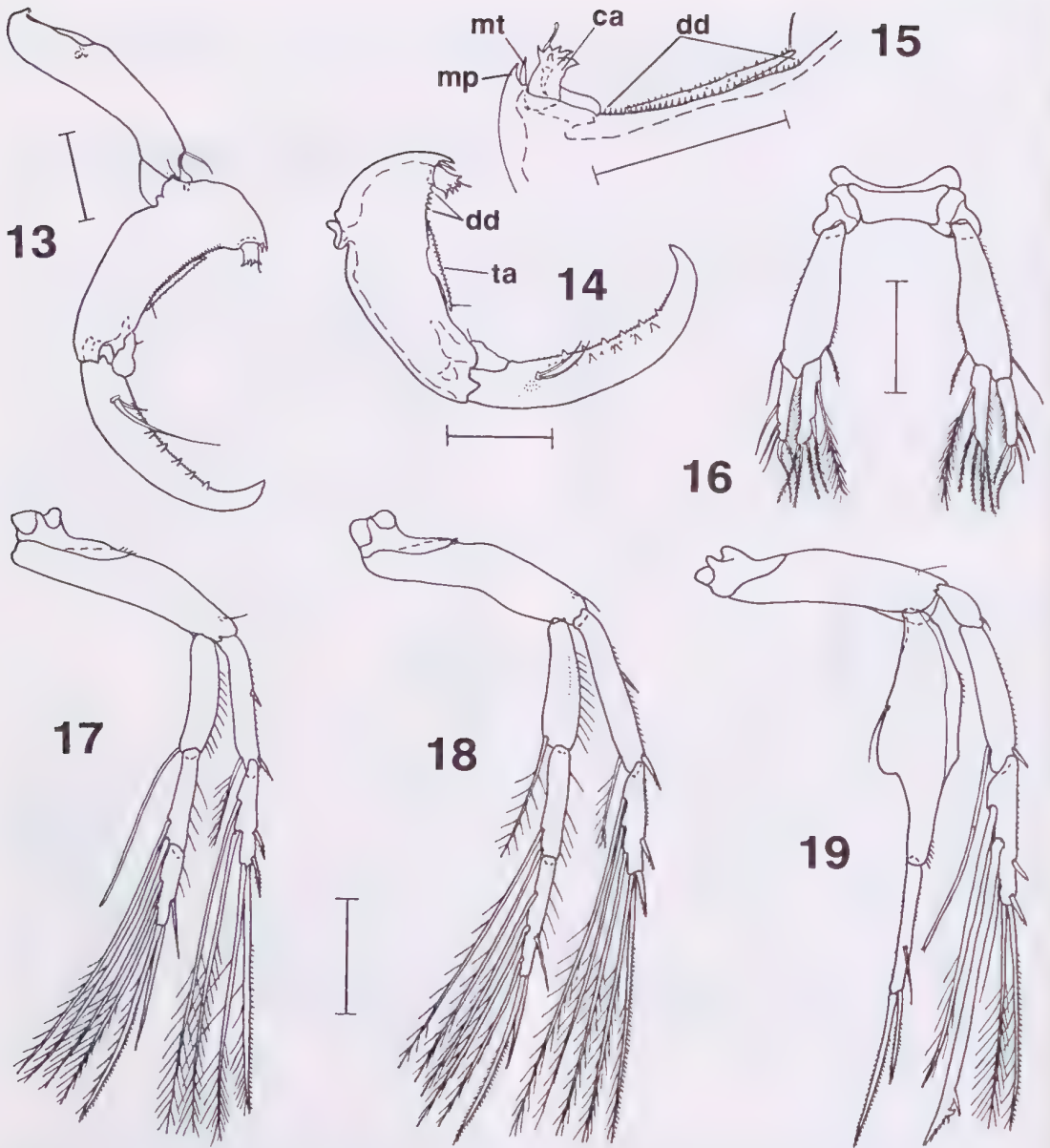
Figures 1–12 *Syngastes dentipes* sp. nov.: 1, lateral aspect, ♀; 2, ventral margin of left cephalic shield, ♀; 3, right A1, anteromedial aspect, ♀; 4, right A2, medial aspect, ♀; 5, right A2-exp, medial aspect, ♀; 6, left Md, medial aspect, ♀; 7, right mandibular gnathobase, medial aspect, ♀; 8, right mandibular palp, medial aspect, ♀; 9, right Mx1, lateral aspect, ♀ (coxa obscured by basis); 10, portion of head capsule with Md, ventral aspect, ♂; 11, portion of head capsule with Mx1, ventral and medial aspect, ♂; 12, Mx2, medial aspect, ♂. Scale lines = 50 μ m.

proximal segment. Claw with two rows of conspicuous teeth; holotype female with four large and three small lateral teeth, and five or six (unilateral variation) large and two or three small medial ones. Area between series of teeth with delicate spines. Two setae on either flank of claw.

P1 as in male (Figure 16), short. Basis 2.4 longer than exopod and about twice as long as endopod.

Basis flattened; medially and laterally each with seta and line of filaments. P1-enp with basalmost, coarsely plumose inner seta inserted at 0.25 relative to length of endopod, succeeding seta at 0.7. Exopod with two serrate apical and three delicately plumose outer setae.

P2 (Figure 17) and P3 (Figure 18) similar in outline, each with short coxa, elongate basis,



Figures 13–19 *Syngastes dentipes* sp. nov.: 13, left Mxp, medial aspect, ♀; 14, right Mxp-enp, lateral aspect, ♀; 15, portion of left Mxp-enp, medial aspect, ♀; 16, pair of P1, anterior aspect, ♂; 17, left P2, anterior aspect, ♀; 18, left P3, anterior aspect, ♀; 19, left P4, anterior aspect, ♀. Scale lines = 50 μm.

slender three-segmented endopod and shorter two-segmented exopod. Coxae distally serrate. Bases with posterior seta. P2 with endopodal segments decreasing in length from 55 μm (enp1) to 35 μm (enp3). Outer edge of endopodal segments lined with filaments, edge of exp-1 with denticles. Setal formula of P2-enp, 1 : 2 : 221 : 0 : 0, of P2-exp, 1 : 222 : 2. Seta on P2-end1 hollow and extending to apex of end3, seta on exp1 shorter, bearing

filaments. Outer setae on P2-exp spiniform and finely serrate. P3-end and P3-exp with 1 : 2 : 321 : 0 : 0 and 1 : 322 : 2 setae. Endopodal segments subequal in length but decreasing in width distally. Posterior flank and outer edge of P2-enp1 lined with filaments. Outer edge of P3-end2 and end3 with filaments, edge of exopodal segments with denticles. Inner setae on enp1 and exp1 plumose and subequal in length.

Basis of P4 (Figure 19) 95 μm long, slightly wider than bases of P2 and P3 and with a posterior lamella on a level with insertion of endopod. Seta inserted at 0.8 relative to length of basis. P4-enp two-segmented, with 1 : 021 : 0 setae. Enp1 112 μm long, 35 μm wide, basal portion lamellar, widest at 0.7, then abruptly narrowing; with carina along posterior flank. P4-enp2 almost cylindrical, 60 μm long and about 6 μm wide. P4-exp three-segmented, segments 22, 67 and 62 μm long respectively. Outer edge of exp2 and exp3 with row of denticles. Suture between exp1 and exp2 distinct only on outer flank. Exp with 0 : 1 : 322 : 1 : 1 setae. Hollow seta on P4-exp2 extends somewhat beyond tip of exopod. Three inner setae on exp3 inserted almost equidistant along margin; basal seta solid, with filaments; next seta strongly sclerotised, 140–150 μm long, with harpoon-like apex; third seta very slender and less than half the length of the other setae. Outer of two apical setae

somewhat stouter than inner seta; outer seta with serrate outer edge and filaments along inner edge; inner seta with filaments on either side.

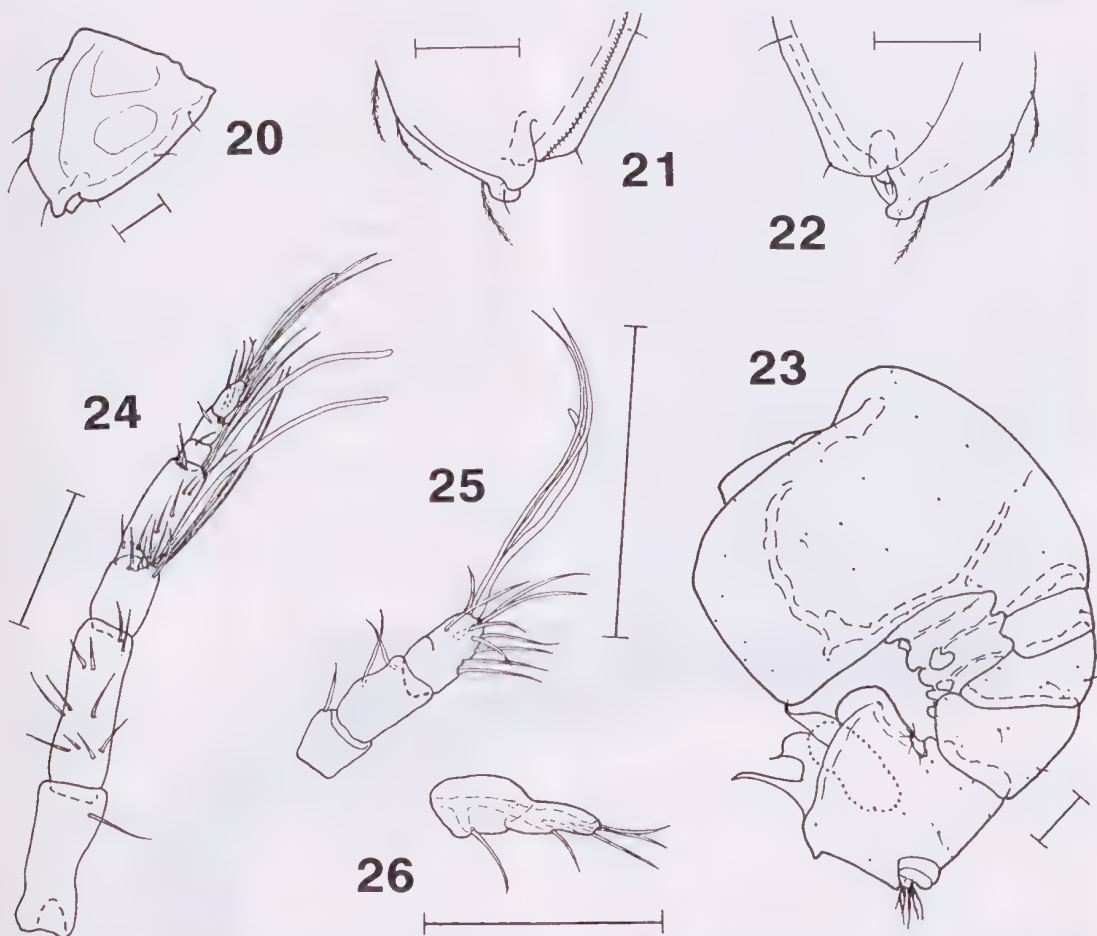
P5 (Figure 20) wide and flattened. Baseoendopod and exopod almost completely fused. Lamellar ventral margin and elongate ridge enclosing narrow groove. Area of baseoendopod with four slender, slightly plumose setae and short setula. Posterior margin of P5 with two ridge-like lamellae which enclose an elongate groove; edges of lamellae (Figure 21) delicately serrate. Posterior margin with three slender setae, apically with two small setae (Figure 22).

Furcal rami 10 μm long; with seven setae, the longest 40 μm long.

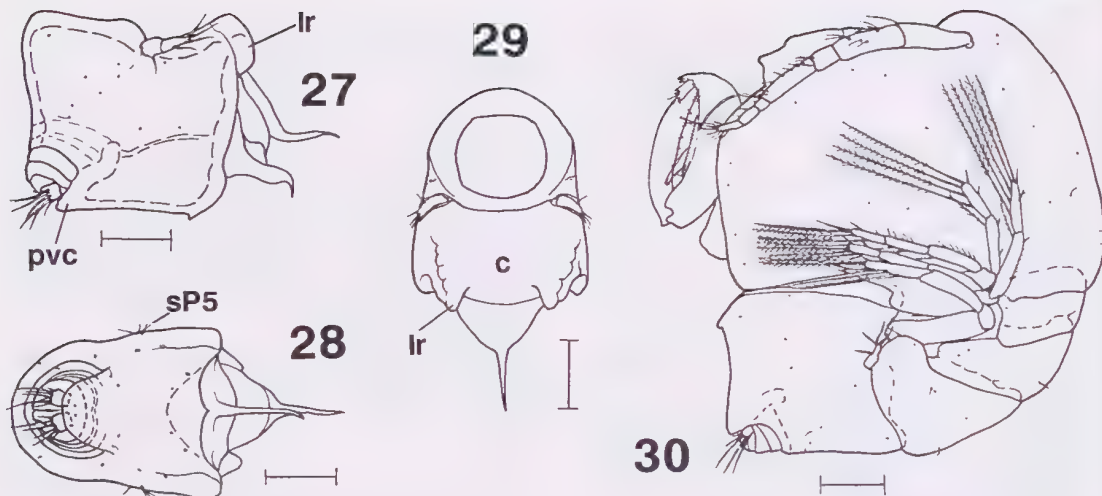
Egg sac with four 120 μm long eggs.

Male

Length 427–458 μm . Ventral margin and posteroventral angle of cephalic shield more



Figures 20–26 *Syngastes dentipes* sp. nov.: 20, left P5, lateral aspect, ♀; 21, posterior portion of right P5, medial aspect, ♀; 22, posterior portion of right P5, lateral aspect, ♀; 23, lateral aspect, ♂; 24, left A1, lateral aspect, ♂; 25, three terminal segments of right A1, lateral aspect, ♂; 26, right P5, lateral aspect, ♂. Scale lines = 50 μm .



Figures 27–30 *Syngastes dentipes* sp. nov., ♂: 27, urosome with P5, lateral aspect from right hand side; 28, urosome posterior aspect; 29, urosome with P5, anterior aspect; 30, lateral aspect. Scale lines = 50 µm.

truncate than in female. With three free thoracic somites (Figure 23), the fourth somite incorporated into genital complex. A1 seven-segmented (Figure 24), segments 55, 62, 30, 45, 12, 15, and 16 µm long. Three apical segments (Figure 25) more slender than basal segments. Aesthetascs on A1–3 and A1–4 4–5 µm wide, that on A1–7 shorter and more slender, 2 µm wide. Number of setae: 1, 11, 10+Ae, 11+Ae, 1, 2, 12+Ae. Outline and setation of A2, Md, Mx1, Mx2 and Mxp as in female. P1–P4 slightly shorter but otherwise similar to those of females.

P5 (Figure 26) 37 µm long, undivided, though suture present between wide basal and elongate distal portion. Basal portion with one seta, distal portion with one basal and three apical setae.

Genital complex of a 434 µm long paratype 135 µm long, 155 µm high. Anterior operculum with long, sharply bent spiniform projection, posterior valve with slender posteriorly bent spine (Figures 27, 28). Posteroventral corner of genital complex extending beyond anal cone. Anterior portion of spermatophore reservoir with pair of lamellar ridges enclosing a cavity (Figure 29).

Remarks

Syngastes dentipes is easily distinguished from other species on the basis of the maxilliped: the wide endopodal segment has a heavily sclerotised cylindrical appendage (instead of a slightly sclerotised semi-spherical or bud-shaped tubercle) and a very elongate and slender tongue-like process; the claw has two rows of teeth. *S. dentipes* is not closely related to any of the species described so far, the female A1 is five-segmented, the second maxillae are very slender and P4-enp bears a single seta.

All tegastids are strongly sclerotised. The cephalic shield in *S. dentipes*, as in other *Syngastes*, is ventrally prolonged so that the maxillipeds can be hidden between these valves. In both females and males of *S. dentipes*, the ventral margin of the enlarged genital segment is armed with a ridge enclosing a narrow groove. In a strongly bent animal, this groove can enclose the posteroventral margin of the cephalosome (Figure 30). The groove on P4-end1 seems to be fitted to enclose the inner edge of exp2. The small epimeral lamellae on the thoracomeres can protect the articulation between bases and exopods of the legs P2–P4.

ACKNOWLEDGEMENTS

The sublittoral substratum was made available to me by P.A. Hutchings which is gratefully acknowledged, and thanks also go to J.W. Reid and V.A. Harris for helpful comments on an earlier draft of this manuscript.

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The Colt Model 1851 Navy revolver and its purchase by the Western Australian Police Force

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The Belt Pistol of Navy size, or, as it is commonly known, the Model 1851 Colt revolver is one of the best known of the various models manufactured by Colt's Patent Firearms Manufacturing Company of Hartford, Connecticut, U.S.A., between 1851 – 1873. Colt's also had a manufacturing facility in London, at Millbank, between 1853 and 1857, and thereafter a sales office in Pall Mall. It is from the Pall Mall depot that many public and private purchases of Colt's revolvers by Australia originated, including the revolvers now under discussion.

THE W.A. POLICE REVOLVER

The Western Australian Museum Arms and Armour Collection possesses a Model 1851 Colt revolver, W513), which is marked on the top of the barrel "Address Col. Colt London". The serial number is 37468, and engraved on the steel buttstrap in script is "Police Force Western Australia" (see Figures 1 and 2). The revolver bears British proof marks and is typical of the variation known as London-London, meaning that it is a London made London type, rather than the London type actually made in the U.S.A. The London type has more rounded screw heads than the U.S. type and also has steel butt straps rather than brass. A check of London production records shows that the year of manufacture was 1856.¹

Research in the state archives resulted in the location of a document from the W.A. Agent General in London, P.G. Julian, to the W.A.

government, dated 18th August 1859. This document advises the W.A. government that three cases, containing "Revolvers and Swords for the Police Force", had been despatched per the "Crystal Palace"² (see Figure 3).

Further search revealed an invoice dated 28th July 1859, from Colts' of Pall Mall, London, to the W.A. government, for two tin-lined cases containing 24 Belt Pistols with spare parts, flasks, holsters and pouches. The government, it is noted on the bottom of the invoice, were charged one shilling for each pistol to have them engraved "Police Force W. Australia"³ (see Figure 4). The third case of the shipment per the "Crystal Palace" is also revealed in the archives. A receipt from Parker, Field and Son of High Holborn, London, dated 9th August 1859, describes 24 Cavalry Swords, with bags, and knots. A note on the invoice informs the W.A. government that they were

¹ Wilson, R.L., "Colt Dates of Manufacture, 1837 – 1978", M. Albert, Victoria, 1983, p.6.

² Battye Library, C.S.O. Correspondence, Acc. 36/419/47.

³ Battye Library, C.S.O. Correspondence, Acc. 36/419/49.

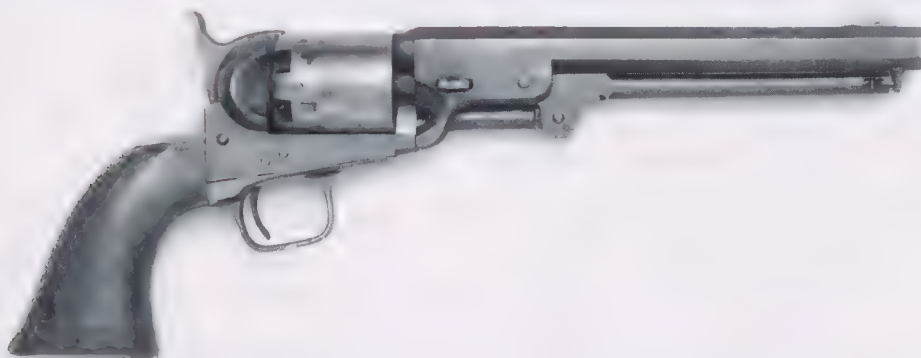


Figure 1 The Colt Model 1851. Manufactured at Colt's premises in London in 1856, it was purchased in a lot of 24 by the Western Australian Police Force in 1859 (Photo D. Elford).

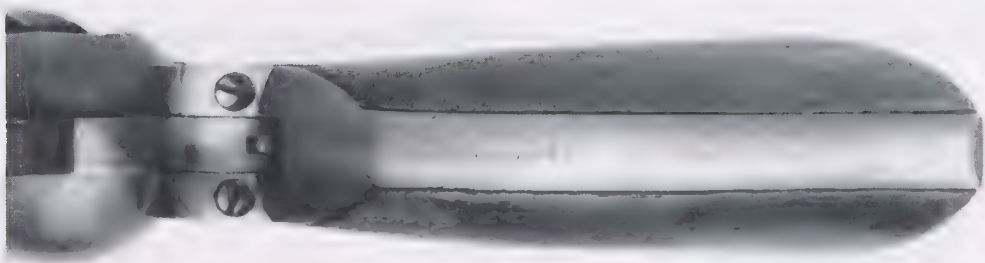


Figure 2 The butt strap of this Colt revolver is engraved "Police Force – Western Australia". Some revolvers from this shipment are engraved "Police Force W. Australia" (Photo D. Elford).

correct "Police Force Western Australia". This shipment was packed in one tin-lined case⁴ (see Figure 5). There is no doubt that the three cases containing revolvers and swords for the Police Force, described in the P.G. Julian advice of 18th August 1859, are these three cases.

No swords by this maker and with this marking are known as yet, but the revolver residing in the W.A. Museum collection is certainly one of the 24 belt pistols ordered in 1859. The engraved legend "Police Force Western Australia" and the place of manufacture, name of manufacturer and date of manufacture all conform to the date of this shipment. The revolver was obviously produced in 1856 and remained in store until ordered by W.A. in 1859.

It was decided to canvas the private and institutional Colt collections in Australia to ascertain whether any other of the 23 companion revolvers had survived. This was done by informal inquiries culminating in telephone contact with eastern states collectors. The result was, including the W.A. Museum revolver, a total of six survivors, and possibly a seventh. It was discovered that many of these revolvers contained mismatched parts, that is, the major components such as frame, butt strap, barrel, cylinder, barrel wedge and loading lever, which are all numbered to conform to the serial number allocated to the frame of the revolver, were found not to match.

The W.A. Museum revolver has a mismatched cylinder, and with three exceptions, all other revolvers are also mismatched (see Table 1). The reason for this mismatching is determined to be probably a result of a Police armourer who was not particular in re-assembling these revolvers when they were sent in for stripping and servicing, or equally possible, they were kept in service for so long that it eventually became necessary to "cannibalise" some to keep the others operative. It is possible of course that these mismatched parts are from revolvers other than police arms, but two factors mitigate against this being the case. Firstly,

of the Australian survivors, all mismatched parts are from a 900 digit range of numbers in the 37,400 – 38,300 serial range of the revolvers themselves. Secondly, if these parts were installed years later from various sources, they would either be unnumbered spare parts, or would include at least one high serial number from revolvers current when these arms were wearing out. It is believed

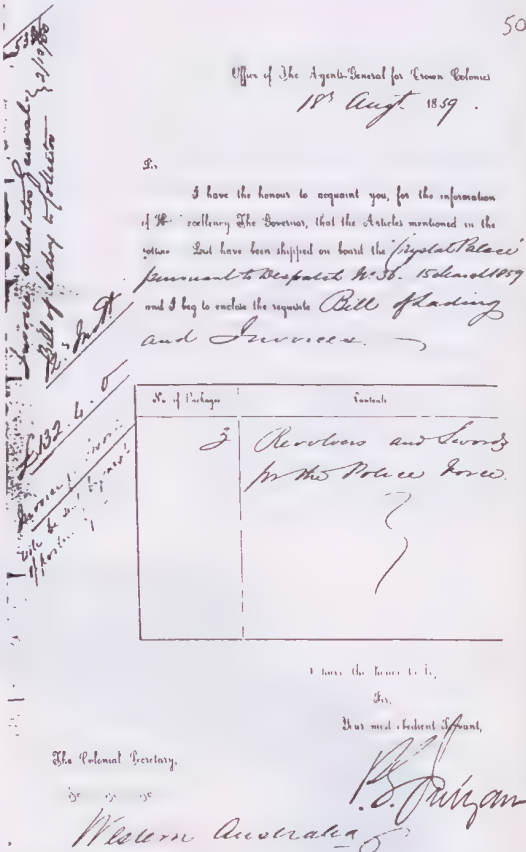


Figure 3 The shipping advice dated 18th August 1859 advising the W.A. Government that three cases of "Revolvers and Swords for the Police Force" have been dispatched (Battye Library).

⁴ Battye Library, C.S.O. Correspondence, Acc. 36/419/47.

Table 1 Serial numbers and markings of known W.A. Police Colt Revolvers.

Location	Revolver no.	Mismatched part	Part no.	Engraved
Western Australia	37468	Cylinder	37598	Western
Western Australia	37434	———— all matching ————		Western
South Australia	37757	Barrel	37813	W.
		Loading lever	37813	
		Cylinder	37408	
		Wedge	38251	
Victoria	37854	———— all matching ————		W.
Victoria	38244	Loading lever	37802	Not stated
New South Wales	37802	———— all matching ————		Not stated
England	37931	Loading lever	17822	W.

Note: The author has inspected the W.A. Museum specimen. All other revolvers are “as reported”.

therefore that all these mismatched numbers came from the 23 companion revolvers of the 1859 shipment. From these parts it is possible to determine the serial numbers of ten of the Police revolvers. They are 37408, 37434, 37468, 37598, 37757, 37802, 37813, 37854, 38244 and 38251. The sixth, New South Wales, revolver is reported to be all matching numbers, yet its serial number, 37802, appears on a loading lever on revolver number 38244. This item is as yet unconfirmed. All other revolvers are reported to be London-London type, British Proved, steel buttstraps and engraved in script, “Police Force Western Australia”, or “Police Force W. Australia”. A seventh revolver has been reported from England. It is engraved “Police Force W. Australia”, and is serial number 37931. The loading lever is serial numbered 17822, the only part not from the police serial range. This English revolver brings the known serial numbers to eleven. It is unknown why there are two

variations in backstrap engravings. Possibly “Western” was a mistake made on a few pistols which was corrected to plain ‘W’ on subsequent arms. Despite this variation there seems to be no doubt that all these revolvers are survivors of the 1859 shipment of 24 Model 1851 Colts.

It has not been possible at this time to uncover any details of history or issue, but the facts presented, even without historical background, still represent an important find of a complete shipment of historic colonial W.A. Police arms. These arms have now been substantially identified, shedding light on the little known London production and colonial purchases. The author would like to acknowledge the assistance of Mr Max Laucke of South Australia.

Manuscript received 13 July 1994; accepted 10 November 1994.

An experimental evaluation of habitat choice in three species of goby (Pisces: Gobiidae)

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The ways in which fish species at similar trophic levels are able to coexist have been examined extensively (see review by Ross 1986 and references therein). However, it is only recently that attempts have been made to use experimental methods to identify the influence that one species may have on the habitat choice of another (e.g., Werner and Hall 1976, 1977; Wiederholm 1987; Magnhagen 1988a, b). While studies of the effects of one species of fish on another in the field have the advantage of providing data on those species in their natural environment, the ability to regulate and manipulate conditions in the laboratory means that laboratory studies can be used to elucidate the role played by individual factors in influencing particular types of behaviour (Crowder 1986). For example, the use of artificial seagrass in laboratory trials provides cover without the confounding effects brought about by the animals and plants usually associated with living seagrass (Bell *et al.* 1985).

Two dominant habitat-types occur in the shallows of Wilson Inlet, a seasonally closed estuary in southwestern Australia, namely unvegetated sand and beds of the aquatic macrophyte *Ruppia megacarpa* (Lukatelich *et al.* 1987), the latter of which may be dense or patchy. The three most abundant demersal species of teleost which occupy these habitats are gobies, each of which shows a greater degree of association with either beds of *Ruppia* or bare sand (Humphries *et al.* 1992; Humphries and Potter 1993). Thus, whereas *Favonigobius lateralis* shows a strong association with bare sand, *Afurcagobius suppositus* and *Pseudogobius olorum* are more often associated with dense and patchy *Ruppia* habitats respectively. Since the above species are all found in the same area in Wilson Inlet, but are associated with different habitat types, a series of laboratory experiments were designed to determine whether the choice of habitat by each of the three goby species is influenced by the presence of either or both of the other species.

The three species were collected from Wilson Inlet and were maintained in 20 l glass aquaria at

ambient photoperiod (13.5 h light/10.5 h dark), temperature (20°C) and salinity (ca 30 ‰) and fed brine shrimp daily. The experiments were conducted in a square tank comprising 1 m long and 0.5 m high sides. Washed sand was placed in the tank to a depth of 5 cm and covered with water to a depth of 35 cm. Artificial seagrass was placed in one half of the tank and the other half was left bare. To ensure even illumination, two fluorescent lights were positioned above the tank, these were perpendicular to the boundary of the artificial seagrass and bare sand. The artificial seagrass, which was designed to resemble *Ruppia megacarpa*, was constructed from 40 cm lengths of olive-green curling ribbon. Each blade was split into four longitudinal strips and stapled on to a wire mesh at a density of 670 'blades' m⁻², a density which simulates the dense *Ruppia* habitat. Prior to experimentation fish were acclimated to the experimental tank for approximately 18 hours, during which time they were not fed. To determine the intervals at which readings should be made, a total of 42 individuals of each species (in groups of 6 individuals) were observed in isolation and the length of time they took to make a 'conspicuous movement' within the experiment tank was noted. A 'conspicuous movement' was one where a fish moved the equivalent of half the length of the tank, i.e., it could have moved from one type of habitat to another. Results showed that, on average, 78% of individuals of each species made a 'conspicuous movement' within 5 minutes.

The number of fish in each habitat was recorded every 5 minutes for one hour in both the morning and afternoon and once every hour for the six hours between these readings. After each hourly reading, the fish's choice of habitat was assessed in response to a disturbance designed to simulate a predator.

All trials were replicated twice, with the combinations randomly assigned to particular days to remove time effects. In the single species experiments, the trials were conducted with densities of 10, 20 and 30 individuals and in those with two or more species, the trials involved 10

individuals of each species. Although the densities recorded in the field were generally at the lower end of the range used for these trials, i.e., 10 individuals m^{-2} (Humphries and Potter 1993), it was considered important to use at least this density to provide a sufficiently large expected frequency for statistical purposes (Sokal and Rohlf 1981). Trials with all combinations of species were conducted: i.e., *P. olorum*/*A. suppositus*, *P. olorum*/*F. lateralis*, *A. suppositus*/*F. lateralis*, *P. olorum*/*A. suppositus*/*F. lateralis*. Each fish was only used once in the experiments.

The G-statistic was used to test results for significant deviation from expected frequencies. This test being theoretically superior and computationally simpler than the χ^2 test (Sokal and Rohlf 1981). Readings and replicates were tested for homogeneity using an 'interaction' or 'heterogeneity' G-test. If all readings were homogeneous, the results were pooled. In only five of the 78 (6.4%) trials carried out were the replicates not homogeneous. In single species trials, observed frequencies were tested against expected frequencies of 50:50 using a goodness of fit G-test and a pooled G-statistic was calculated. For mixed species trials, observed frequencies were tested against the frequencies obtained using the same number of fish as in single species trials, using a G-test for independence. This type of comparison means that the only difference between the single species experiments and those involving mixed species was the addition of another species.

When on their own *A. suppositus* showed a very strong preference for the seagrass, irrespective of the densities of fish or the time of day. A similar, but less pronounced, choice was generally exhibited by *F. lateralis*. *Pseudogobius olorum* showed no consistent preference for either habitat. In mixed species experiments, *A. suppositus* maintained its strong preference for seagrass, whereas *F. lateralis* reversed its choice of habitat to that of sand in the presence of *A. suppositus*. *Pseudogobius olorum* showed a clear preference for a particular habitat, namely seagrass, only when all three species were together. In all combinations all species sought refuge in the seagrass when disturbed.

In these laboratory experiments, the habitat choice of *A. suppositus* and *P. olorum* when on their own paralleled their distribution in the field, i.e., in both the laboratory and the field *A. suppositus* showed a very strong preference for the artificial seagrass, while in the case of *P. olorum* the lack of any consistent preference for either seagrass or sand in the laboratory is consistent with the greatest densities for this species being recorded from patchy *Ruppia* habitat in the field (Humphries and Potter 1993). In contrast, although *F. lateralis* chose artificial seagrass in the laboratory it was only ever recorded at low densities in *Ruppia* in the

field (Humphries and Potter 1993), while in other systems both Shaw (1986) and Bell and Westoby (1986) reported that *F. lateralis* was typically associated with a bare sand habitat.

In the mixed species experiments, the choice of habitat by each of these species was significantly influenced by the presence of other species. The most dramatic effect was seen with *F. lateralis*, which showed a significant increase in the utilisation of sand in the presence of *A. suppositus*. This parallels the distribution of these species in the field and also the situation reported by Wiederholm (1987) for another goby species (*Pomatoschistus microps*), which when alone utilised artificial vegetation, but in mixed species experiments and in the field was found in an open habitat. However, although Wiederholm (1987) reported a shift in habitat utilisation and considered that the small size of *P. microps* may make it vulnerable to displacement by larger, more aggressive species, other workers have found that differences in habitat use are maintained both in the absence and presence of species at the same trophic level and are probably more a function of differences in morphology and species-specific responses to environmental factors (Schlosser and Toth 1984). A comparison of the body lengths in the present study suggests that size alone cannot account for changes in habitat choice. While *A. suppositus* is on average the largest of the three goby species and therefore could conceivably win agonistic interactions with *F. lateralis* if size was the sole criterion, it did not affect the habitat choice of *P. olorum*, the smallest of the three species. Furthermore, the presence of *F. lateralis* appeared to lead to a greater number of *A. suppositus* entering the artificial seagrass. Thus, there would appear to be a mutual interaction between *F. lateralis* and *A. suppositus*. The fact that *A. suppositus* shows a very strong preference for seagrass would probably make it difficult to displace from this habitat. Humphries and Potter (1993) reported that not only did *Afurcagobius suppositus* and *F. lateralis* share several dietary taxa but that they were one of only two pairs amongst three gobiid and three atherinid species whose diets were often correlated. Moreover, the similar morphology of the terminal/superior mouths, along with short guts and ambush-type feeding strategy of *A. suppositus* and *F. lateralis* contrast with the sub-terminal mouth, long gut and active omnivorous foraging mode exhibited by *P. olorum* (Gill and Miller, 1990; Gill, 1993; Gill and Potter 1993). These similarities may make competitive interactions more likely between *A. suppositus* and *F. lateralis* than between these species and *P. olorum*.

ACKNOWLEDGEMENTS

The authors are indebted to Stuart Bradley, Mike

Calver and Ron Wooller for advice in the early stages of this work. We would also like to thank Stuart Bradley, Ian Potter, Glenn Hyndes, Margaret Platell and Gerry Allen for critically reviewing the manuscript. The use of Murdoch University facilities are greatly appreciated.

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Manuscript received 13 July 1994; accepted 21 December 1994.

First record of the false catshark, *Pseudotriakis microdon*, from Australian seas

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The shark family Pseudotriakidae is distributed worldwide, mainly in deep waters of continental slopes. Two species were formerly recognised, but Compagno (1984) placed the Indo-Pacific *Pseudotriakis acrales* Jordan and Snyder, 1904 in the synonymy of the Atlantic *P. microdon* Capello, 1868.

The known distribution of *P. microdon* consists of widely scattered, mainly Northern Hemisphere locations, including off the northeastern United States, Iceland, France, Portugal, Madeira, Azores, Senegal, Cape Verde Islands, Japan, Taiwan, and the Hawaiian Islands. Prior to the first Australian record reported below, the only locations in the Southern Hemisphere were New Zealand and the Aldabra Islands group, just north of Madagascar.

Most of the specimens taken thus far were captured by deep-set longlines or occasionally by bottom trawlers. Depth of capture ranged between 200 and 1500 metres.

The first Australian record reported herein was captured on 10 August 1994 by the South Australian trawler "Lucky S". It was fishing for orange roughy (*Hoplostethus atlanticus*) on the continental shelf in the extreme southwestern corner of Australia off Cape Leeuwin (approximately 35°00'S, 114°45'E). Depth of capture was 830 m and a bottom temperature of 6° C was recorded.

The trawler's crew did not recognise the unusual catch and it was taken back to Albany. Fortunately, Mr Mike Jones, of Allerton Bait Supplies, notified the Albany Residency Museum. Val Milne, Head Curator of the institution, arranged to have it frozen and shipped to the Western Australian Museum in Perth.

The shark was photographed, preserved in

formalin, and is now lodged in the collection of the Western Australian Museum (registration number P.30826–001).

Compagno (1984, part 2) provided diagnostic information, an outline drawing, and a brief summary of the biology of *P. microdon*. In part 1 of this same work he gave detailed illustrations of the measurements and explained the terminology which is used in the following paragraph.

The following measurements (in cm) were recorded when the specimen was freshly thawed: total length 200.0; precaudal length 174.0; prenarial length 10.7; preoral length 10.1; preorbital length 14.5; prespiracular length 22.3; prebranchial length 34.0; head length 44.5; prepectoral length 45.5; prepelvic length 127.0; vent-caudal length 87.0; pre-first dorsal length 86.0; pre-second dorsal length 148.0; interdorsal space 22.0; dorsal-caudal space 8.3; pelvic-anal space 17.5; anal-caudal space 6.2; eye length 4.6; eye height 2.2; interorbital space 14.0; nostril width 2.7; internarial space 10.7; anterior nasal flap length 0.8; mouth length 8.0; mouth width 23.8; first gill slit height 4.3; second gill slit height 4.9; third gill slit height 4.9; fourth gill slit height 4.8; fifth gill slit height 3.7; caudal peduncle height 9.6; girth 74.5; pectoral anterior margin 23.8; pectoral base 11.3; pectoral height 23.8; pelvic anterior margin 14.4; pelvic base 13.8; pelvic height 14.4; pelvic inner margin length 7.2; pelvic posterior margin length 12.7; first dorsal anterior margin 45.0; first dorsal base 41.5; first dorsal height 5.8; first dorsal inner margin 4.1; second dorsal anterior margin 29.4; second dorsal base 29.0; second dorsal height 15.8; second dorsal inner margin 4.1; second dorsal posterior margin



Figure 1 *Pseudotriakis microdon*, 200 cm TL, off Cape Leeuwin, Western Australia.

14.7; anal length 22.5; anal anterior margin 19.4; anal base 19.0; anal height 9.8; anal inner margin 4.1; anal posterior margin 9.9; dorsal caudal margin 39.0; preventral caudal margin 19.0; posterior caudal margin 29.0; terminal caudal margin 8.5; subocular pocket depth 0.8; second dorsal origin-anal origin 8.8; intergill length 12.1; abdomen height 29.5; tail height 18.0; pelvic-caudal space 41.0; subterminal caudal margin 6.9; pectoral-pelvic space 69.0; spiracle height 4.1; spiracle width 1.5.

An examination of the stomach of the specimen

revealed no discernable food items as digestion had reduced all contents to a liquid.

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Manuscript received 26 August 1994; accepted 22 December 1994.

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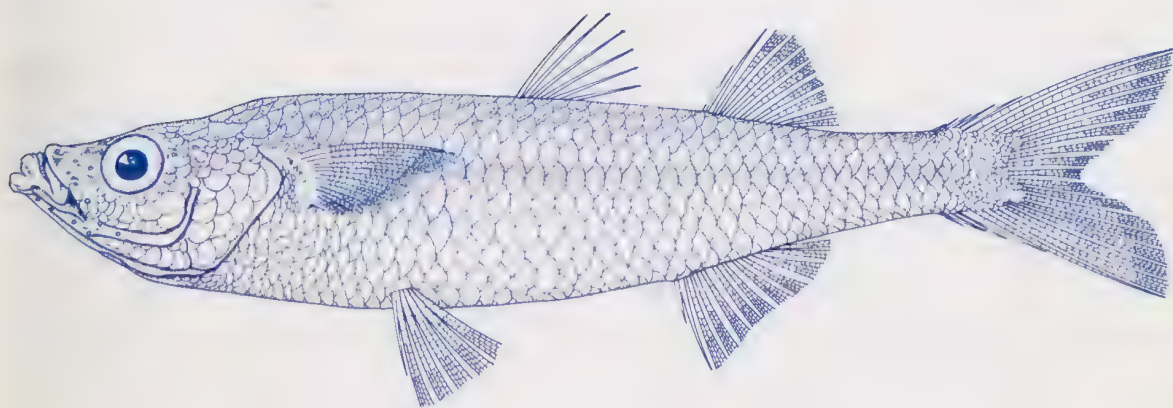
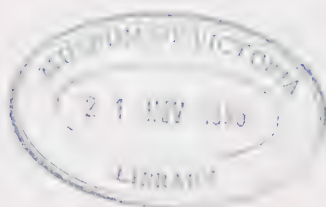
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Records of the Western Australian Museum



Volume 17 Part 3 1995

Records of the Western Australian Museum

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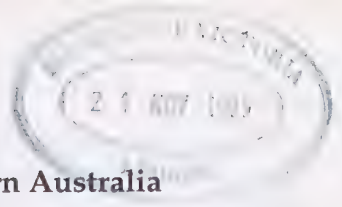
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Printed and published by the Western Australian Museum
© Western Australian Museum, October 1995
ISSN 0312 3162

Cover: Line drawing of *Craterocephalus fistularis* sp. nov.
Illustration by Barbara Duckworth.



Biological inventory of Koolan Island, Western Australia 1. Flora and vegetation

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Abstract - A total of 282 plant taxa have been recorded from five major vegetation units on Koolan Island at the head of the Yampi Peninsula. This represents over a quarter of the flora recorded for the Fitzgerald Botanical District. A total of 12 new naturalised weeds were recorded from the island. The closure of the iron ore mine on Koolan Island and the removal of the town will provide opportunities to study both weed invasion and persistence and the establishment of a large permanent wetland in a sub-humid tropical environment.

INTRODUCTION

A biological survey of Koolan Island was undertaken over a week during the wet season of February 1993. This survey was supplemented by herbarium records and previous collections by KFK and AAM. This paper describes the flora and vegetation of the island, while a subsequent paper will describe the island's fauna. This work will provide a benchmark against which to measure the rehabilitation of the island following closure of the major iron ore mine in October 1993 after 29 years of operation. Despite a long history of exploration and mining on the island its flora and vegetation have been little studied, with the earliest collections in the Western Australian Herbarium (PERTH) dating from the mid 1960s (also see Beard 1979).

STUDY AREA

Koolan Island is located 130 km north of Derby at the northern end of the Yampi Peninsula. It is separated from the mainland by a channel 1 km wide. The island is 13 km long and 5.5 km wide at its widest point, with the long axis of the island orientated NW – SE (Figure 1). Koolan is one of the many islands of the Buccaneer Archipelago. This area experiences a monsoonal climate with an annual rainfall of about 960 mm with most falling between December and March. Mean summer temperatures for Derby (some 130 km to the south) range from 35 to 37 degrees with high relative humidities (Bureau of Meteorology 1975).

The island is essentially a series of parallel flat-

topped ridges formed from steeply dipping beds of the resistant Warton and Pentecost Sandstones and a series of deeply incised creeks through softer Elgee Siltstone (Tyler and Griffin 1993). The adjacent mainland has essentially similar geology and geomorphology. The basal part of the Pentecost Sandstone on Koolan Island is composed of high grade haematite (iron ore) and was mined from 1965 until 1993.

This ore proved to be of very high grade (average 65% iron) with over 50 million tonnes having been extracted. A smaller mine operated on nearby Cockatoo Island between 1957 and 1986. The main pit on Koolan Island is 1.5 km long, 45 m wide and was mined at the eastern end to a depth of 80 m below sea level. This pit will fill with fresh water from a natural aquifer once mining operations cease.

The town associated with this mine was located at the eastern end of the island and had a population of 850 people. Most of the towns people left in October 1992 with complete closure planned by October 1993. It is planned that all buildings will be removed and all road surfaces removed and ripped. Only the airstrip will be left intact.

METHODS

During the wet season survey most of the field work was concentrated on the eastern two thirds of the island along roads and down creek lines. The area of Warton Sandstone along the southern edge of the island, supporting very open eucalypt woodland (Figure 1), was not visited due to time

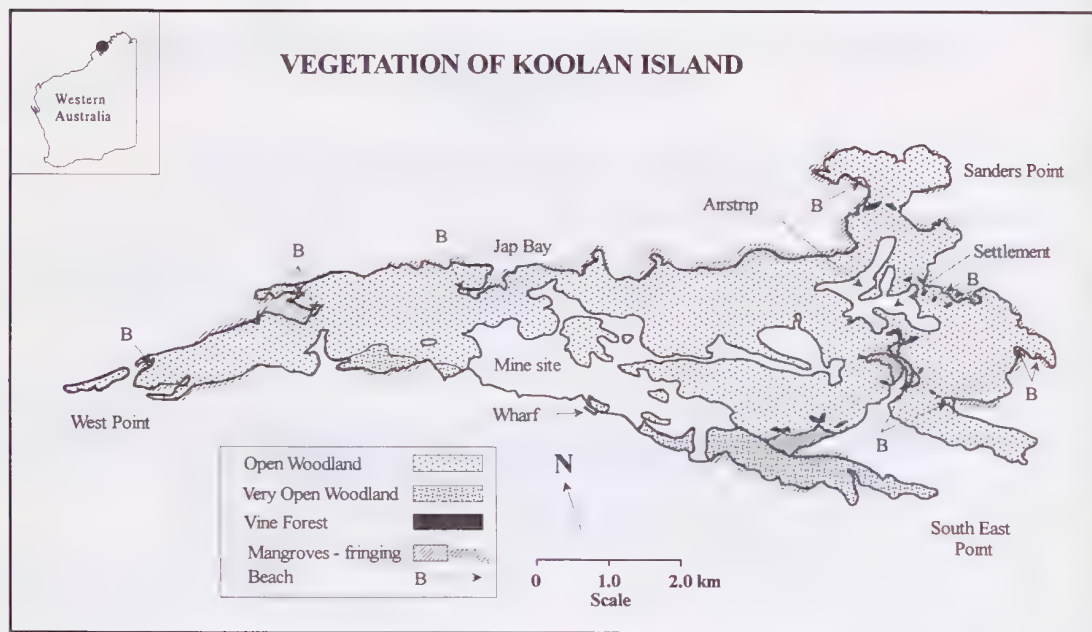


Figure 1 Map of Koolan Island, showing major vegetation types and location of town, airstrip and mine.

and access limitations. Voucher collections were made of all fertile plants found and notes made on their distribution and abundance. While detailed searches were undertaken for naturalised weed taxa, due to time limitations no attempt was made to record all exotic taxa found in the townsite. Vouchers were lodged in PERTH. Nomenclature largely follows Wheeler *et al.* (1992). Additional records were available from previous visits by KFK and AAM as well as other collections lodged in PERTH.

A structural vegetation map was compiled from field notes and a 1: 30 000 colour mosaic based on August 1992 photography (Figure 1).

RESULTS AND DISCUSSION

Flora

Two hundred and eighty-two taxa (species, subspecies and varieties) were recorded from 79 families. Forty-three of these were exotic taxa from 19 different families; three of these families (Moringaceae, Solanaceae and Turneraceae) were only represented by introduced taxa. The most well represented families were the Poaceae (22 native, 11 naturalised taxa), Papilionaceae (15 native, 5 naturalised taxa), Euphorbiaceae (15 native, 3 naturalised taxa), and Myrtaceae (11 native taxa) (Appendix 1). Species composition clearly shows the tropical nature of the flora with high proportions of grasses and Euphorbiaceae. It

is, however, a sub-humid tropical flora sharing only 12% of the evergreen tropical flora of Christmas Island (Gentili 1972, Du Puy 1993). Approximately half of the species co-occurring between the two islands are pan-tropical weeds.

Koolan Island falls on the western margin of the Fitzgerald Botanical District which covers some 83,330 km² (Beard 1979). The flora of this area is still poorly known. Hnatiuk (1990) recorded 842 taxa from this region while the recently completed Kimberley Flora (Wheeler *et al.* 1992) record 1030 taxa. The present survey has added a further 24 taxa. Thus, 27 % of the flora of the entire Fitzgerald Botanical District has been recorded on Koolan Island although the island represents less than 0.1% of the land area of this District.

Weeds

Several weed taxa were largely restricted to the six steep gullies north and south of the townsite down which the treated sewage was discharged (Figure 2). In particular *Euphorbia cyathophora* and *Clitoria ternatea* were common and locally dominant in the bottoms of these gullies. In Creeks 1 and 2 on the north side of the settlement *Senna alata*, a garden escape, has become wide spread, reaching heights of 4 m. This is the first record of this species naturalised in Western Australia. It is also naturalised in the Darwin area. Another garden escape which has become widespread along the road verges and in the creeks is *Turnera*

ulmifolia, a small yellow flowering herb. This taxa has also not previously been recorded elsewhere in Western Australia.

In a vegetated valley near the southern boundary of the town site, a small but vigorous population of rubber vine (*Cryptostegia madagascariensis*) was found. The creek line running south from this valley (Creek 4) was dominated by *Leucaena leucocephala*. The Poinciana (*Delonix regia*) was also found in this area and is the first time this taxon has been recorded as naturalised in Western Australia. The *Leucaena leucocephala* and *Delonix regia* were also found in the two smaller creek lines (Creeks 5 and 6) at the south west end of town.

Eleven species of grass have become naturalised including buffel grass (*Cenchrus ciliaris*). This species has become a very serious weed at Cape Range (near Exmouth) where it was planted along the coastal flats as improved pasture and has subsequently spread through most of the plant communities of the area (Keighery and Gibson 1993).

Currently all the weeds are restricted to the settlement area (including creek lines and sewerage outfalls) and road verges. With closure of the town supplementary irrigation and sewerage output will cease. This is likely to lead to long term loss of weed taxa given the extended dry season in this area. Weedy tree species may persist but success of

further recruitment is uncertain. Experience in areas such as Cape Range suggests some of the exotic grasses will persist. The current distribution of *Cryptostegia madagascariensis* elsewhere in Australia suggests that this species will also persist and spread unless efforts are made to eradicate it. It should be noted that of the several hundred taxa present in the town gardens, only 44 have become naturalised (Appendix 1).

Vegetation

Five major vegetation units were found on the island. There were also several minor units but these occupied areas too small to map (Figure 1).

The most widespread community was the *Eucalyptus miniata* - *Eucalyptus confertiflora* open woodlands generally over *Triodia* hummock grassland. The understorey was composed of a diverse herb layer with species such as *Tacca leontopetaloides* and *T. maculata* being common. The density of shrubs in this community is variable but several species of *Terminalia* and *Acacia* are common (Appendix 1). This vegetation type covers about 80% of the non-disturbed area of the island and is the common vegetation type on the adjacent mainland (Beard 1979). The floristics of this community are fairly consistent, however there is considerable local change in dominance across the island. This floristic variation did not appear to be

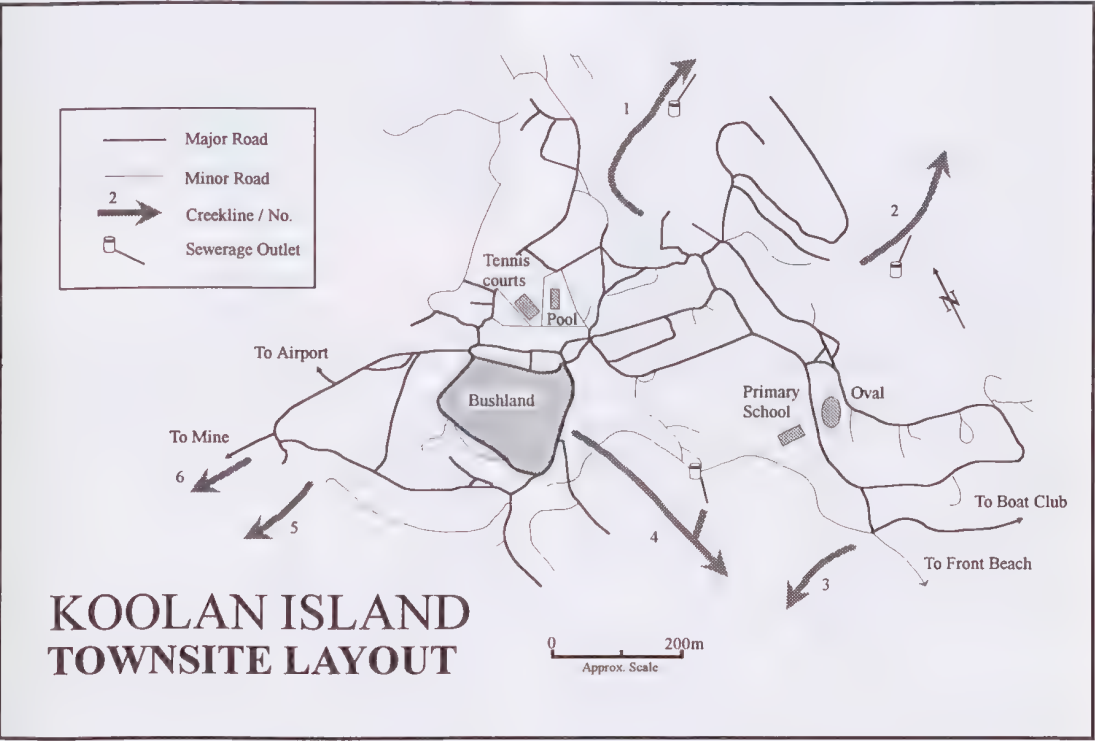


Figure 2 Map of the townsite showing location of creek lines and sewerage outfalls.

correlated to slope or aspect and occurred on both the Pentecost Sandstone and the Elgee Siltstone. In places it gave way to small groves of *Callitris intratropica* with understoreys dominated by *Calytrix exstipulata*. This community type has previously been recorded on the nearby Cockatoo, Irvine, Bathurst and Kingfisher Islands (previously known as the Wood Islands) some 30 km to the east on the same lithologies (Burbidge *et al.* 1978; K.F. Kenneally, unpub).

Aerial photographs show a very open eucalypt woodland along the southern edge of the island coincident with the Warton Sandstone (Tyler and Griffin 1993). This area was not surveyed due to both time and access limitations. Woodlands on this substrate type have been described for Augustus, Heywood, Champagny, Unwins and Saint Andrew Islands of the Bonaparte Archipelago lying some 130 km to the north east (Burbidge *et al.* 1978) and for an area in the proposed Prince Regent National Park (Miles *et al.* 1975). The composition of the woodlands on the Warton Sandstone is similar to the *Eucalyptus miniata* - *Eucalyptus confertiflora* open woodlands described above, but commonly also including *Eucalyptus perfoliata*, *Plectrachne pungens*, and less commonly *Eucalyptus ferruginea* and *Acacia stipulosa*.

Large mangrove communities occur in two sheltered bays south of the settlement. In addition, much of the coastline of the island supports a narrow mangrove fringe (Figure 1). Four species of mangrove were recorded from the large stand immediately south of the settlement: *Avicennia marina*, *Camptostemon schultzei*, *Excoecaria agallocha* and *Rhizophora stylosa*. The mangrove communities are small and species poor compared to the much more extensive mangrove stands on the nearby mainland (Kenneally 1982).

Small patches of vine forest dominated by *Canarium australianum* were found in the steep creek lines on the eastern end of the island (Figure 1). Patch size ranges from just a few trees to several hectares in extent. The patches shown in Figure 1 are those that were visited on the ground and / or were discernible on the photo-mosaic. There are undoubtedly more smaller patches than could be mapped at this scale. Koolan Island is at the south western edge of the main area of occurrence of rainforest in the Kimberley. The only patches further to the south west are those on the northern shore of King Sound and the coastal areas of the Dampier Peninsula (McKenzie 1991).

More than 1500 patches of rainforest are scattered across the Kimberley. These range in size from a few tree crowns to more than 100 ha (McKenzie 1991). Kenneally *et al.* (1991) in a study of 99 Kimberley rainforests (largely vine forest) recorded 575 species. Only one of these species was endemic to the rainforest, with most species

occurring widely in a number of habitats across northern Australia. The reason for the widespread nature of most of these species appears to be both their ability to cope with nutrient-poor substrates and propagule dispersal by birds and bats (McKenzie 1991). Our data are consistent with this hypothesis. One hundred and one of the 575 species recorded from Kimberley rainforest patches are found on Koolan Island.

Koolan Island shares 45.5 and 52.1% of the taxa recorded from the two closest rainforest patches studied by Kenneally *et al.* (1991) (02/3 and 25/3 on Yampi Peninsula, some 50 km to the east south east, with 33 and 46 species respectively). These data further indicate the widespread nature of the Kimberley rainforest flora.

Twelve small beaches occurred in protected bays around Koolan Island. Most of the beaches are adjacent to mangrove community but, in addition, a distinct community develops on the mobile sands. Common components of these beach communities include *Spinifex longifolius*, *Commelina ensifolia*, *Ipomoea pes-caprae* and *Abrus precatorius*. Two beaches to the south east of the settlement and another north of the airfield were frequently used by the residents for recreation and were serviced by gravel roads.

Minor vegetation units include the narrow fringing vegetation of *Melaleuca viridiflora* along some of the larger creek lines, and the *Callitris intratropica* stands. Species-poor haematite scree communities, seen at several locations. These were dominated by combinations of trees and / or shrubs. Common species included *Callitris intratropica*, *Canarium australianum*, *Pouteria sericea*, *Vitex acuminata* and *Pavetta kimberleyana*. All of these units are restricted to a few hectares in extent.

DISCUSSION

The flora and vegetation of Koolan Island is very similar to both the adjacent mainland and nearby Cockatoo Island. It is a sub-humid tropical sandstone flora which is widespread across northern Australia. Twelve new naturalised weeds for Western Australia were recorded from the island (*Allamanda cathartica*, *Antigon leptopus*, *Cascabela thevetia*, *Cassia fistula*, *Delonix regia*, *Gliricidia sepium*, *Moringa oleifera*, *Peltophorum pterocarpa*, *Ruellia tuberosa*, *Senna alata*, *Tecoma stans*, *Turnera ulmifolia*). *Antigon leptopus*, *Delonix regia*, *Tecoma stans*, and *Turnera ulmifolia* are also common weeds on Christmas Island.

One native species was found to be restricted to Koolan Island. This was an apparently undescribed species of smooth, white barked eucalypt (*E. aff. cadophora* Keighery and Gibson 15 and 95). This taxon was found occasionally across the island.

None of the native taxa reached their range ends on Koolan Island.

Koolan Island presents a excellent opportunity for long term monitoring of weed invasion and persistence following major disturbance in an isolated sub-humid tropical environment. The townsite will also allow an opportunity to study the fate of the introduced garden species following the removal of town infrastructure and supplementary watering.

One major new habitat created by the mine will be an extensive, deep permanent freshwater wetland in the bottom of the major pit (next to the loading jetty, Figure 1) which has intersected a shallow aquifer. We are unaware of any similar habitat on the sandstone areas of the adjacent mainland. The colonisation of this wetland will add significant numbers of new taxa to the flora of the island. At the date of the present survey the pit was bare of all vegetation and water levels were being kept artificially low by continuous pumping.

ACKNOWLEDGEMENTS

We would like to thank Norm McKenzie (CALM) who organised the 1993 field trip and assisted with data collection, and Patrick Warrant (BHP) who assisted in arranging accommodation and transportation on the island. Mike Lyons prepared the figures, Daphne Edinger assisted in compiling the flora list and processing specimens, and the database personnel of the WA Herbarium helped with data extraction. The Department of Environment, Science and Technology partially funded this work under the National Rainforest Program. A.A. Mitchell's work was undertaken during surveys for exotic species as part of the Northern Australian Quarantine Strategy.

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Manuscript received 3 January 1995; accepted 30 March 1995.

APPENDIX 1

Flora list of 282 taxa recorded from Koolan Island, Western Australia. Collection numbers refer to specimens lodged in PERTH. * indicates a naturalised weed and "sr" indicates a sight record.

Family Acanthaceae

Dicliptera armata F.Muell.

Hypoestes sp.

* *Ruellia tuberosa*

Vernon 40

Vernon 51

L. Mitchell 3118

Family Adiantaceae

- Cheilanthes brownii* (Kuhn) Domin Keighery / Gibson 249
Cheilanthes caudata R.Br. Keighery / Gibson 250
Cheilanthes sieberi Kunze Keighery sr
Cheilanthes tenuifolia (Burm.f.) Sw. Keighery sr

Family Aizoaceae

- Sesuvium portulacastrum* (L.) L. Keighery sr
Zaleya galericulata (Melville) H. Eichler Keighery sr

Family Amaranthaceae

- Achyranthes aspera* L. Keighery sr
Amaranthus pallidiflorus F. Muell. Keighery sr
* *Amaranthus viridis* L. Keighery / Gibson 131
Gomphrena sp. Keighery / Gibson 128
Ptilotus exaltatus Nees in Lehm. Keighery / Gibson 210
Ptilotus fusiformis (R.Br.) Steud. var. *gracilis* (R.Br.) Benth. Vernon 43

Family Anacardiaceae

- Buchanania obovata* Engl. Kenneally sr

Family Apiaceae

- Trachymene didiscoides* (F. Muell.) B. L. Burt Fryxell 3915, Vernon 06

Family Apocynaceae

- * *Allamanda cathartica* L. Keighery / Gibson 91
* *Cascabela thevetia* L. Mitchell 3116, Keighery / Gibson 28
* *Catharanthus roseus* (L.) G. Don Keighery / Gibson 30
Tabernaemontana pandacaqui Lam. Keighery / Gibson 47
Wrightia saligna (R.Br.) Benth. Vernon 23, Keighery / Gibson 02, 211

Family Asclepiadaceae

- Cynanchum carnosum* (R.Br.) Schltr. Keighery / Gibson 46
Cynanchum puberulum F. Muell. ex Benth. Vernon 62
Gymnema stenophyllum A. Gray Keighery / Gibson 134
Marsdenia viridiflora R.Br. Keighery / Gibson 62
Sarcostemma viminalis subsp. *australe* (R.Br.) P. I. Forst. Vernon sn
Secamone timoriense Decne. Keighery / Gibson 40
Tylophora flexuosa R.Br. Keighery / Gibson 88
* *Cryptostegia madagascariensis* Bojer ex Decne. Mitchell 2276, 3117, Keighery / Gibson 26

Family Asparagaceae

- Protasparagus racemosus* (Willd.) Oberm. Keighery sr

Family Asteraceae

- * *Bidens bipinnata* L. Kenneally sr, Keighery sr
Chrysogonum eclipioides (F. Muell.) F. Muell. Kenneally sr
Pterocaulon sphacelatum (Labill.) F. Muell. Vernon 72
* *Tridax procumbens* L. Marchant 72/1, Keighery / Gibson 129
Vernonia cinerea (L.) Less. Vernon 20, k127

Family Avicenniaceae

- Avicennia marina* (Forssk.) Vierh. Keighery / Gibson 212

Family Bignoniaceae

- Dolichandrone heterophylla* (R.Br.) F. Muell. Keighery / Gibson 105
* *Tecoma stans* (L.) Juss. ex Kunth Keighery / Gibson 32

Family Bombacaceae

- Camptostemon schultzei* Mast. Keighery sr

Family Boraginaceae

- Heliotropium glabellum* "yellow variant" Keighery sr
Heliotropium glabellum R.Br. Sands 4984, 4976, Keighery / Gibson 145
Trichodesma zeylanicum (Burm.f.) R.Br. Keighery sr

Family Burseraceae	
<i>Canarium australianum</i> F.Muell.	Keighery/Gibson 48, 68, 136
Family Byblidaceae	
<i>Byblis liniflora</i> Salisb.	Vernon 31
Family Caesalpiniaceae	
* <i>Cassia fistula</i> L.	Mitchell sr
<i>Chamaecrista mimosoides</i> (L.)Greene	Keighery/Gibson 213
* <i>Delonix regia</i> (Bojer ex Hook.) Rafin.	Keighery/Gibson 59
<i>Erythrophleum chlorostachys</i> (F.Muell.)Baill.	Vernon 12
<i>Lysiphyllum cunninghamii</i> (Benth.)de Wit	Vernon 04
* <i>Peltophorum pterocarpa</i> (DC)Backer ex K. Heyner	Keighery sr
* <i>Senna alata</i> (L.)Roxb.	Keighery/Gibson 77, Mitchell 3111
<i>Senna goniodes</i> (A.Cunn.ex Benth.)Randell	Vernon 42, Keighery/Gibson 109
Family Capparaceae	
<i>Capparis lasiantha</i> R.Br.ex DC.	Keighery/Gibson 214, 248
<i>Capparis sepiaria</i> L.	Keighery sr
<i>Capparis spinosa</i> L. var. <i>nummularia</i> (DC.)Bailey	Vernon 64
<i>Cleome viscosa</i> L.	Keighery sr
Family Caryophyllaceae	
<i>Polycarpaea spirostylis</i> F.Muell.	Keighery sr
Family Celastraceae	
<i>Denhamia obscura</i> (A.Rich.)Meisn.	Keighery/Gibson 215A, 215B
Family Chenopodiaceae	
<i>Salsola kali</i> L.	Kenneally sr
<i>Suaeda arbusculoides</i> L.S.Sm.	Keighery sr
Family Combretaceae	
<i>Terminalia canescens</i> (DC.)Radlk.	Vernon 27, Keighery/Gibson 41
<i>Terminalia latipes</i> Benth. subsp. <i>psilocarpa</i> Pedley	Vernon 10, Keighery/Gibson 87
<i>Terminalia platyphylla</i> F.Muell.	Keighery sr
Family Commelinaceae	
<i>Cartonema spicatum</i> R.Br.	Vernon 30, Keighery/Gibson 247
<i>Commelina ensifolia</i> R.Br.	Vernon 29, Keighery/Gibson 37
<i>Murdannia graminea</i> (R.Br.)G.Brueckn.	Vernon 38
Family Convolvulaceae	
<i>Evolvulus alsinoides</i> (L.)L.	Vernon 33
<i>Ipomoea</i> sp.	Vernon 48
<i>Ipomoea pes-caprae</i> (L.)R.Br.	Keighery sr
* <i>Ipomoea quamoclit</i> L.	Mitchell 2272, Keighery/Gibson 05,
<i>Jacquemontia paniculata</i> (Burm.f.)Hallier	Vernon 47, Fryxell 4598,
	Keighery/Gibson 119
* <i>Merremia dissecta</i> (Jacq.)Hallier	Keighery/Gibson 50
<i>Operculina brownii</i> Ooststr.	Fryxell 4607
<i>Polymeria ambigua</i> R.Br.	Keighery/Gibson 113
<i>Xenostegia tridentata</i> (L.) D.Austin et Staples	
subsp. <i>hastata</i> (Desr.) Ooststr.	Keighery/Gibson 216
Family Cucurbitaceae	
* <i>Cucumis melo</i> L. subsp. <i>agrestis</i> (Naudin)Grebensc.	Keighery/Gibson 57
<i>Mukia maderaspatana</i> (L.)M.Roem.	Keighery sr
<i>Trichosanthes cucumerina</i> L. var. <i>cucumerina</i>	Keighery/Gibson 135
Family Cupressaceae	
<i>Callitris intratropica</i> (F.Muell.)R.T.Baker and H.G.Sm.	Keighery/Gibson 67
Family Cyperaceae	
<i>Cyperus bulbosus</i> M.Vahl	Keighery/Gibson 217
<i>Fimbristylis cymosa</i> R.Br.	Keighery/Gibson 94, 150

- Family Dilleniaceae
Hibbertia oblongata R.Br.ex DC. Vernon 57, Fryxell 4592,
 Keighery / Gibson 112
- Family Dioscoreaceae
Dioscorea bulbifera L. Keighery / Gibson 17
- Family Droseraceae
Drosera lanata Kondo Keighery sr
Drosera petiolaris R.Br.ex DC. Vernon "a"
- Family Ebenaceae
Diospyros maritima Blume Keighery / Gibson 31, 152
- Family Elatinaceae
Bergia pusilla Benth. Keighery / Gibson 289
- Family Euphorbiaceae
Croton sp. Keighery sr
Breynia cernua (Poir.)Muell.Arg. Keighery / Gibson 110
Bridelia tomentosa Blume Vernon 02
Euphorbia australis Boiss. Keighery sr
Euphorbia coghlani Bailey Keighery sr
* *Euphorbia cyathophora* Murray Keighery / Gibson 04, Handasyde 01
Euphorbia drummondii Boiss. Keighery sr
* *Euphorbia hirta* L. Keighery / Gibson 06
Euphorbia kimberleyensis B.G.Thomson Fryxell 4582
Excoecaria agallocha L. Keighery / Gibson 55
Flueggea virosa (Willd.)F.Voigt subsp. *melanthesoides*
 (F.Muell.)G.L.Webster Keighery / Gibson 156
* *Jatropha gossypifolia* L. Keighery / Gibson 100
Petalostigma pubescens Domin Vernon 22, Keighery / Gibson 66, 218
Petalostigma quadriloculare F.Muell. Mitchell 2280, 3114
Phyllanthus amarus Schumach. Keighery / Gibson 44
Phyllanthus maderaspatensis L. Keighery / Gibson 19
Phyllanthus virgatus G.Forst. Keighery / Gibson 54
Sebastiania chamaelaea (L.)Muell.Arg. Vernon 21, Keighery / Gibson 121
- Family Goodeniaceae
Goodenia sepalosa F.Muell.ex Benth. Vernon 19, Fryxell 4599,
 Mitchell 2265, Keighery / Gibson 20
Scaevola macrostachya (de Vriese)Benth. Vernon 07, Keighery / Gibson 157
- Family Gyrocarpaceae
Gyrocarpus americanus Jacq. Keighery sr
- Family Haloragaceae
Gonocarpus leptothecus (F.Muell.)Orchard Keighery / Gibson 219A
- Family Lamiaceae
Anisomeles malabaricum (L.)R.Br.ex Sims Mitchell 3112
* *Hyptis suaveolens* (L.)Poit. Keighery sr
- Family Lauraceae
Cassytha aurea J.Z.Weber Keighery / Gibson 153
Cassytha capillaris Meisn. Keighery / Gibson 149
Cassytha filiformis L. Keighery sr
- Family Loganiaceae
Mitrasacme connata R.Br. Vernon 36
Strychnos lucida R.Br. Keighery sr
- Family Loranthaceae
Amyema bifurcata (Benth.)Tiegh. Keighery / Gibson 291
Amyema miquelii (Lehm.ex Miq.)Tiegh. Keighery sr
Amyema thalassium Barlow Keighery / Gibson 147
Decaishnina sp. Keighery sr

- Dendrophthoe acacioides* (Benth.) Tiegh.
Diplatia grandibractea (F. Muell.) Tiegh.
Lysiana spathulata (Blakely) Barlow subsp. *spathulata*
 Keighery/Gibson 65, 106A
 Keighery/Gibson 25
 Keighery/Gibson 155
- Family Lythraceae
Lagerstroemia archeriana Bailey
 Keighery sr
- Family Malvaceae
Abutilon aff. *oxycarpum* (F. Muell) F. Muell. ex Benth.
Abutilon andrewsianum W. Fitzg
Abutilon indicum (L.) Sweet
Gossypium costulatum Tod.
 Keighery/Gibson 158
 Vernon 54
 Keighery/Gibson 33
 Vernon 28, Fryxell 3861, 4619,
 Mitchell 2278, Lullfitz sn
 Mitchell sr
 Mitchell 3115
 Vernon 55, Keighery/Gibson 53, 159
 Keighery sr
- * *Gossypium hirsutum* L.
Hibiscus aff. *fryxellii* Mabb.
Hibiscus leptocladus Benth.
Thespesia thespesioides (Benth.) Fryxell
- Family Meliaceae
Owenia vernicosa F. Muell.
 Keighery/Gibson 111
- Family Menispermaceae
Tinospora smilacina Benth.
 Keighery sr
- Family Mimosaceae
Acacia ampliceps Maslin
Acacia hippuroides Heward ex Benth.
Acacia holosericea A. Cunn. ex G. Don
Acacia multisiliqua (Benth.) Maconochie
 Keighery/Gibson 108
 Vernon 04, Vernon 55, Sands 4973
 Kenneally sr
 Vernon 01, Fryxell 4605, Sands 4975,
 Lakeman 2, Keighery/Gibson 45
 Done 730, Keighery/Gibson 106, 219
 Vernon 09, White 09, Keighery/Gibson
 142, Sands 4946
 Vernon 70, Kenneally 8531, Sands 4950
 Keighery/Gibson 18
 Keighery/Gibson 12
- Acacia* sp. (sec. *juliflorae*)
Acacia stigmatophylla A. Cunn. ex Benth.
- Acacia tumida* F. Muell. ex Benth.
 * *Leucaena leucocephala* (Lam.) de Wit
Neptunia gracilis Benth.
- Family Moraceae
Ficus opposita Miq.
Ficus virens Aiton
 Keighery/Gibson 49
 Kenneally sr
- Family Moringaceae
 * *Moringa oleifera* Lam.
 Keighery/Gibson 230
- Family Myrtaceae
Calytrix brownii (Schauer) Craven
Calytrix exstipulata DC.
Eucalyptus aff. *cadophora*
Eucalyptus confertiflora F. Muell.
Eucalyptus dampieri D.J. Carr and S.G.M. Carr
Eucalyptus miniata A. Cunn. ex Schauer
Eucalyptus perfoliata R. Br ex Benth.
Eucalyptus rupestris Brooker and Done
Eucalyptus sp. B (Kimb flora)
Eucalyptus tectifera F. Muell.
Melaleuca viridiflora Sol. ex Gaertn.
 Vernon 69, Fryxell 4601
 Keighery/Gibson 09
 Keighery/Gibson 15, 95
 Vernon 14, Keighery/Gibson 148
 White 11
 Kenneally sr
 Kenneally sr
 Done 737
 Keighery/Gibson 10
 Vernon 18
 Keighery/Gibson 11
- Family Nyctaginaceae
Boerhavia sp.
Boerhavia dominii Meikle and Hewson
 Keighery sr
 Keighery/Gibson 83, 146
- Family Oleaceae
Jasminum didymum G. Forst.
 Fryxell 4585
- Family Papilionaceae
Abrus precatorius L.
Alysicarpus vaginalis (L.) DC.
 Keighery sr
 Keighery/Gibson 52

- Cajanus viscidus* Maesen
Canavalia rosea (Sw.)DC.
Christia australasica (Schindler)
 Bakh. f. et van Meeuwen
 * *Clitoria ternatea* L.
Crotalaria montana Roth
Desmodium filiforme Zoll. and Moritzi
 * *Desmodium tortuosum* (Sw.)DC.
Galactia tenuiflora (Klein ex Willd.)Wight and Arn.
 * *Gliricidia sepium* (Jacq.)Kunth ex Walp.
Gompholobium subulatum Benth.
Indigofera ? *polygaloides* M.Scott
Indigofera sp. A (Kimb Flora)
 * *Macroptilium lathyroides* (L.)Urb.
 * *Stylosanthes guianensis* (Aubl.)Sw.
Templetonia hookeri (F.Muell.)Benth.
Tephrosia leptoclada Benth.
Tephrosia sp.
Vigna lanceolata Benth.
- Fryxell 4586, Vernon 56, Mitchell 3109
 Fryxell 4587, Keighery/Gibson 84, 122
- Keighery/Gibson 220
 Keighery/Gibson 130
 Vernon 50, Keighery/Gibson 120
 Fryxell 4596
 Keighery/Gibson 114, Mitchell 2267, 2275
 Fryxell 4614
 Mitchell 2277, Handysyde 02
 Vernon 58, Keighery/Gibson 24A
 Keighery/Gibson 229
 Keighery/Gibson 70
 Mitchell 2271
 Keighery/Gibson 27
 Vernon 05, Keighery/Gibson 123
 Vernon 15
 Vernon 49, Vernon 52
 Vernon 61
- Family Passifloraceae**
Adenia heterophylla (Blume)Koord.
 * *Passiflora foetida* (L.)
 var. *hispida* (DC. ex Triana and Planchon) Killip
- Keighery/Gibson 137
 Keighery sr
- Family Philydraceae**
Philydrum lanuginosum Gaertn.
- Keighery sr
- Family Poaceae**
Alloteropsis semialata (R.Br.)Hitchc.
Bothriochloa pertusa (L.)A.Camus
 * *Cenchrus ciliaris* L.
 * *Cenchrus echinatus* L.
Cenchrus elymoides F.Muell.
 * *Cenchrus setiger*
 * *Chloris barbata* (L.)Sw.
 * *Chloris gayana* Kunth
Chloris sp.
Chrysopogon latifolius S.T.Blake
Chrysopogon sp.
Cynodon dactylon (L.)Pers.
 * *Dactyloctenium aegyptium* (L.)Willd.
Digitaria bicornis (Lam.)Roem. and Schult.
 * *Echinochloa colona* (L.)Link
 * *Eleusine indica* (L.)Gaertn.
Eragrostis tenella (L.)Roem. and Schult.
Eriachne avenacea R.Br.
Eriachne sulcata Hartley
Heteropogon contortus (L.)P.Beauv. ex
 Roem. and Schult.
Panicum decompositum R.Br.
Paspalum scrobiculatum L.
Plectrachne bymoei C.E.Hubb.
 * *Rhynchelytrum repens* (Willd.)C.E.Hubb.
 * *Setaria pumila* (Poir.)Roem. and Schult.
Sorghum ecarinatum Lazarides
Sorghum plumosum (R.Br.)P.Beauv.
Spinifex longifolius R.Br.
Sporobolus virginicus (L.)Kunth
Triodia sp.
 * *Urochloa mosambicensis* (Hack.)Dandy
Urochloa subquadripa (Trin.)R.D.Webster
Whiteochloa cymbiformis (Hughes)B.K.Simon
- Keighery/Gibson 290
 Mitchell 2269
 Keighery sr
 Grey sn, Keighery/Gibson 133
 Keighery/Gibson 107
 Keighery/Gibson 132
 Keighery/Gibson 116
 Mitchell 2266
 Keighery/Gibson 51
 Keighery/Gibson 102
 Keighery/Gibson 228
 Keighery sr
 Keighery sr
 Keighery sr
 Mitchell sr
 Keighery/Gibson 56, 58
 Keighery/Gibson 126
 Vernon 35, Fryxell 3918
 Vernon 71
- Vernon 73
 Keighery/Gibson 35, 154
 Keighery/Gibson 34
 Vernon 66
 Vernon 65, Keighery/Gibson 115
 Mitchell 2268
 Fryxell 3913
 Keighery/Gibson 151
 Keighery sr
 Keighery sr
 Keighery/Gibson 141, 144
 Keighery/Gibson 74
 Keighery/Gibson 138
 Mitchell 2273
- Family Polygalaceae**
Comesperma secundum Banks ex DC.
- Vernon 60, Fryxell 4609

Family Polygonaceae	
* <i>Antigon leptopus</i> Hook. and Arnd.	Mitchell 3113
Family Portulacaceae	
<i>Calandrinia uniflora</i> F.Muell.	Keighery sr
<i>Portulaca oleracea</i> L.	Keighery sr
<i>Portulaca pilosa</i> L.	Keighery/Gibson 39
Family Proteaceae	
<i>Grevillea agrifolia</i> Cunn. ex R. Br.	Vernon 01, Keighery/Gibson 143
<i>Grevillea cunninghamii</i> R.Br.	Vernon 02, Marchant 72/12, White 08, Fryxell 4590
<i>Grevillea pyramidalis</i> A.Cunn.ex R.Br.	Vernon 03A
<i>Grevillea refracta</i> R.Br.	Vernon 03B
<i>Persoonia falcata</i> R.Br.	Keighery/Gibson 14
<i>Stenocarpus</i> sp. A (Kimb Flora)	Keighery/Gibson 221
Family Rhizophoraceae	
<i>Ceriops tagal</i> (Perr.)C.B.Rob.	Keighery/Gibson 223
<i>Rhizophora stylosa</i> Griff.	Keighery/Gibson 222
Family Rubiaceae	
<i>Aidia racemosa</i> (Cav.)D.D.Tirveng.	Keighery/Gibson 101
<i>Canthium</i> sp. A (Kimb Flora)	Keighery/Gibson 16
<i>Oldenlandia corymbosa</i> L. var. <i>corymbosa</i>	Keighery/Gibson 125A
<i>Pavetta kimberleyana</i> ST Reynolds	Keighery/Gibson 92
<i>Spermacoce leptoloba</i> Benth.	Vernon 41
Family Rutaceae	
<i>Boronia lanuginosa</i> Endl.	Fryxell 4600
Family Santalaceae	
<i>Exocarpos latifolius</i> R.Br.	Fryxell 4608
<i>Santalum lanceolatum</i> R.Br.	Keighery sr
Family Sapindaceae	
<i>Atalaya hemiglauc</i> a (F.Muell.)F.Muell.ex Benth.	Keighery sr
<i>Distichostemon hispidulus</i> (Endl.)S.T.Reynolds var. <i>phyllopterus</i> (F.Muell.)S.T.Reynolds	Vernon 25, White 10
<i>Dodonaea lanceolata</i> F.Muell. var. <i>lanceolata</i>	Vernon 67
Family Sapotaceae	
<i>Mimusops elengi</i> L.	Keighery/Gibson 104
<i>Pouteria sericea</i> (Aiton)Baehni	Keighery/Gibson 23a
Family Scrophulariaceae	
<i>Lindernia</i> aff. <i>clausa</i> (F. Muell.)F. Muell.	Vernon 34
<i>Stemodia lythrifolia</i> F.Muell.ex Benth.	Marchant 72/6
<i>Striga curviflora</i> (R.Br.)Benth.	Vernon 37
Family Solanaceae	
* <i>Physalis minima</i> L.	Fryxell 3920, Keighery/Gibson 103
Family Sonneratiaceae	
<i>Sonneratia alba</i> Sm.	Keighery sr
Family Stackhousiaceae	
<i>Stackhousia intermedia</i> Bailey	Vernon 44
Family Sterculiaceae	
<i>Brachychiton diversifolius</i> R.Br.	Keighery/Gibson 07
<i>Brachychiton viridiflorus</i> (W.Fitzg.)Guymer	Keighery/Gibson 08
<i>Brachychiton viscidulus</i> (W.Fitzg.)Guymer	Fryxell 4591, Keighery/Gibson 63
<i>Melhania oblongifolia</i> F.Muell.	Vernon 53
<i>Melochia umbellata</i> (Houtt.)Stapf	Fryxell 3922, Keighery/Gibson 140
<i>Waltheria indica</i> L.	Vernon 17

Family Stylidiaceae	
<i>Stylidium</i> aff. <i>leptorrhizum</i> F. Muell.	Fryxell 4583, Vernon 59, Vernon sn
Family Taccaceae	
<i>Tacca leontopetaloides</i> (L.) Kuntze	Keighery / Gibson 117
<i>Tacca maculata</i> Seem.	Vernon 26
Family Tiliaceae	
<i>Corchorus leptocarpus</i> (A.Cunn.) Benth.	Fryxell 4595, Keighery / Gibson 22
<i>Grewia breviflora</i> Benth.	Keighery / Gibson 139, 224
<i>Grewia retusifolia</i> Kurz	Vernon 11, 25a, Keighery / Gibson 43
<i>Triumfetta plumigera</i> F. Muell.	Vernon 39, Fryxell 3919, 4616
<i>Triumfetta</i> sp.	Keighery / Gibson 21
<i>Triumfetta</i> sp.	Keighery / Gibson 86
<i>Triumfetta</i> sp. O (Kimb Flora)	Fryxell 3921
<i>Triumfetta</i> sp. S (Kimb Flora)	Vernon 63, Fryxell 4581
Family Turneraceae	
* <i>Turnera ulmifolia</i> L.	Keighery / Gibson 01, 118, Mitchell 2274
Family Typhaceae	
<i>Typha domingensis</i> Pers.	Keighery sr
Family Ulmaceae	
<i>Celtis philippensis</i> Blanco	Keighery / Gibson 225
Family Verbenaceae	
<i>Callicarpa candicans</i> (Burm.f.) Hochr.	Keighery / Gibson 03
<i>Clerodendrum floribundum</i> R.Br. var. <i>coriaceum</i> (R. Br.) Mold.	Vernon 45, Keighery / Gibson 124
<i>Clerodendrum tomentosum</i> (Vent.) R.Br. var. <i>lanceolatum</i> (F. Muell) Munir	Vernon 68
<i>Premna acuminata</i> R.Br.	Keighery / Gibson 90, 226, 227
<i>Stachytarpheta cayennensis</i> (Rich.) Vahl	Mitchell 3110
<i>Vitex acuminata</i> R.Br.	Vernon 08, Keighery / Gibson 23, 29, 81
<i>Vitex glabrata</i> R.Br.	Vernon 13
Family Violaceae	
<i>Hybanthus auranthiacus</i> (F. Muell. ex Benth.) F. Muell.	Keighery / Gibson 13
<i>Hybanthus enneaspermus</i> (L.) F. Muell.	Vernon 46
Family Vitaceae	
<i>Ampelocissus acetosa</i> (F. Muell.) Planch.	Keighery sr
<i>Cayratia trifolia</i> (L.) Domin	Keighery / Gibson 80
<i>Cissus adnata</i> Roxb.	Keighery sr
Family Zygophyllaceae	
<i>Tribulopsis angustifolia</i> R.Br.	Keighery / Gibson 125

Biological inventory of Koolan Island, Western Australia 2. Zoological notes

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Abstract – In terms of its biota, Koolan is the most thoroughly inventoried island on the Kimberley coast. We provide annotated lists of the animal species known from the island: three earthworms, eight land snails, two scorpions, one centipede, nine spiders, two ants, 34 butterflies, one amphibian, 35 reptiles, 116 birds and 18 mammals. In addition, the W.A. Museum holds unsorted collections of moths and beetles. A range of animals have been introduced, including an earthworm *Dichogaster bolau*, a land snail *Laevicaulis alte*, an ant (*Monomorium destructor*), a cockroach and four mammals including the feral goat (*Capra hircus*). Koolan's indigenous fauna is a sub-set of taxa known from the adjacent mainland, although the blind snake *Ramphotyphlops yampiensis*, and the land snails *Kimboraga koolanensis* and *Amplirhagada astuta*, appear to be endemic to the island. The bird list was accumulated during 10 years of monthly observations, but data on other components of the island's fauna are uneven because of sampling artefacts, with a bias towards large land snails, large butterflies and snakes. Nevertheless, the richness of these groups indicates that the numerous rugged sandstone islands along this tropical sub-humid coastline support complex faunas.

INTRODUCTION

Koolan is the only Kimberley island with a long history of invertebrate and vertebrate collection. While the earliest record we can find is of the land snail *Kimboraga koolanensis* described by Iredale (1939), most collections have been made since 1965.

Broken Hill Pty Ltd developed an iron ore mine on the island during the 1960's. By 1985 there were 150 houses and nearly 900 residents, and a range of exotic plants and animals had been introduced. Fortunately, domestic cats and un-sterilised female dogs were forbidden.

The geology of Koolan is described in Tyler and Griffin (1993). The island has an area of 2580 hectares. Its Proterozoic sandstone lithology is expressed as rugged slopes, ridges and uplands mantled with rock scree and shallow skeletal soils that support savanna woodland communities of eucalypts over hummock grass. The coast is steep with narrow gullies and frequent embayments, but few beaches.

Koolan has a tropical sub-humid climate. It receives an average of about 960 mm of rainfall annually. The "Wet" usually extends from December to April, although most rain falls in January, February and March. Virtually no rain falls from May to November.

Data on of the island's indigenous animals were accumulated gradually by island residents and occasional visitors. This opportunistic pattern of

sampling has left gaps in our knowledge of the island's vertebrates and macro-invertebrates, particularly among the relatively immobile taxa likely to be most affected by introduced species. The only systematic biological surveys were monthly bird observations made by one of the authors (L.F.) over the period 1983 to 1993.

From 9 to 15 February 1993, two botanists and one zoologist from CALM collected plants, earthworms, land snails, reptiles and bats to reduce this sampling bias. The field work was carried out just a few months after the mine closed to provide a basis for monitoring the persistence of indigenous and introduced species; the town and mine infrastructure were being dismantled at the time.

This paper reviews the zoological data available from Koolan. Keighery *et al.* (1995) present the corresponding botanical data.

METHODS

The majority of the zoological voucher specimens from Koolan were collected opportunistically by BHP employees resident on the island. Most are lodged at the Western Australian Museum, but some Koolan land snail specimens are held by the American Museum and the Chicago Field Museum of Natural History (Solem 1985).

A search of the invertebrate registers at the W.A. Museum revealed that L. Vernon (= L.F.), O.

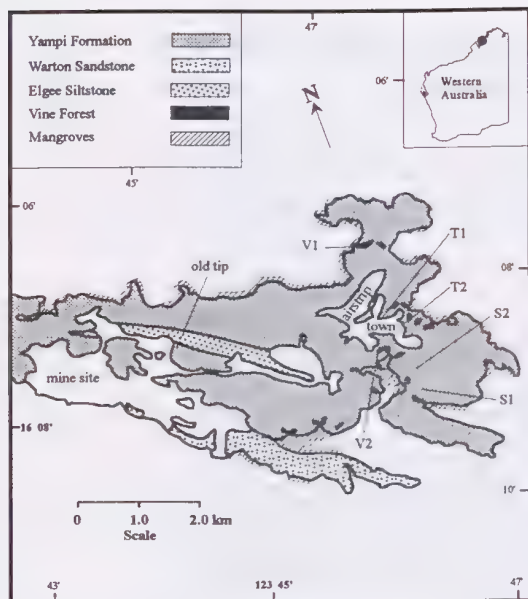


Figure 1 Eastern end of Koolan Island, showing principal 1993 collecting sites.

Milton, F.C. van Ingen and W.H. Butler collected a range of arachnid, myriapod and insect specimens from Koolan between 1965 and 1990. The bulk of these invertebrate collections remain to be identified; only the butterflies and the registered specimens of arachnids and myriapods are listed herein. Butterfly nomenclature follows Common and Waterhouse (1981). The butterflies were identified by M.R. Williams; we have incorporated the records listed by Koch and van Ingen (1969) and Koch (1975) although the relevant specimens have neither museum registration numbers nor field collection numbers.

The February 1993 field work was carried out at the height of the "Wet", when most tropical plants flower and set seed (Wheeler *et al.* 1992). This is also the best time to collect the region's indigenous earthworms. Kimberley earthworms aestivate deep in the soil profile during the six- to eight-month dry season; they are active near the surface only during the "wet" (McKenzie and Dyne 1991). There were heavy rains during the fieldwork in February 1993; soil profiles on Koolan were damp to moist. A total of 28 earthworm quadrats (cf McKenzie and Dyne 1981) were sampled in the range of habitats on the eastern part of the Island: savanna woodlands, rainforest patches (semi-deciduous vine thickets), house gardens, and along a creek on the north side of town. Additional grab samples of earthworms were taken in town to increase the number of taxonomic vouchers. The earthworms were identified by Geoff Dyne (Department of the

Environment, Sport and Tourism, Canberra). Land snails were sought opportunistically in two vine thickets and in town; earlier records were gleaned from taxonomic literature. The land snails were identified by Vince Kessner (Adelaide River, Northern Territory).

The W.A. Museum holds reptile and mammal specimens collected by island residents such as N. Lindus (from 1981 to 1993), L. Vernon (= L.F., 1983 – 1993), G. A. Robinson (1961), O. Milton (1965 – 7), F.C. van Ingen (1965 – 74). Specimens were also contributed by visitors such as W.H. Butler (June 1965 and November 1973), B. Maryan and D. Robinson (August 1992) and other biologists during brief visits. During our February 1993 field work on Koolan, we used mist nets and ultrasound recorders to survey bats that were foraging in the savanna woodlands, mangroves and town. Bats were also sought in their day-roosts in caves and buildings. We set traps for non-volant mammals in the savanna woodlands and along the edge of the mangroves and foot of the scree slope near site V2 (Figure 1), and made nighttime spotlighting traverses along the island's road network. In contrast, our approach to sampling amphibians and reptiles was entirely opportunistic.

Reptile taxonomic names follow Ehmann (1992); Numbers prefixed with "R" or "M" in the vertebrate species lists refer to specimen registration numbers at the W.A. Museum. Other specimen numbers in brackets relate to data from animals captured during the 1993 survey, but subsequently released.

One of the authors, Lee Fontanini (= L.F.) lived on Koolan Island from 1983 to 1993. The bird list herein summarises her 10 years of monthly observations in terms of species' seasonal presence, abundance and habitat-use. Nomenclature follows the Blakers *et al.* (1984). Mangroves around Koolan are either narrow fringes or difficult to reach, so her visits were infrequent (once or twice per year) and restricted to the stands in "Barramundi Bay", south of town. These are by far the largest stands on the island.

Latitude and longitude coordinates cited in the text were measured from the "Yampi" 1 100 000 series topographic map.

RESULTS

Earthworms

We recorded two indigenous species belonging to the genus *Diplotrema*, and an introduced species *Dichogaster bolau* (Michaelsen) that was only found in town gardens. In contrast, *Diplotrema* were common in the vine thickets, scarce in the savanna woodlands, and were not found in the townsite. To confirm the scarcity of earthworms in the

Table 1 Location and habitat of the sites that were systematically sampled for earthworms (see Figure 1).

Site	Location (°S, °E)	Geology ^a	Habitat	No. specimens
V1	16°07'00", 123°46'50"	Pky	vine thicket	9
V2	16°08'15", 123°46'40"	Pky	vine thicket	4
S1	16°08'50", 123°46'45"	Pky	savanna woodland	0
S2	16°08'40", 123°46'50"	Pky	savanna woodland	1
T1	16°08'00", 123°46'45"	Pky	swampy creek	0
T2	16°08'10", 123°46'45"	Pky	town gardens	20+

^aPky = Yampi Formation, comprising quartz, hematitic and feldspathic sandstone, siltstone and quartz conglomerate that, on Koolan Island, lies unconformably over Elgee Siltstone (Pke) (Tyler and Griffin 1993).

savanna woodlands, N.McK. dug more than 50 shallow potholes in valley floors, slopes and uplands north of the "old tip" (Figure 1) during our last two days on the island; no earthworms were found. The results of the formal, quadrat-based earthworm survey are summarised in Tables 1 and 2.

Land Snails

Subulinidae

Erelopeas interioris (Tate). Two dead shells were found under sandstone rocks in vine thicket V2 in February 1993 (see Table 1).

Helicarionidae

Westralcystis lissus (E.A. Smith). Two dead shells were found under sandstone rocks in vine thicket V2 (Feb. 1993).

Camaenidae

Torresitrachia bathurstensis (E.A. Smith). One dead juvenile was taken from soil on the bottom of a concrete culvert under the road near the workshop complex (Feb. 1993). Six dead shells

were found under sandstone rocks in vine thicket V2 (Feb. 1993).

Amplirhagada astuta (Iredale). The holotype (AM C.64857) was collected on Koolan Island. D. Milton sent additional specimens to the W.A. Museum in August 1966. On 14 February 1993, two were found crossing path in town after heavy rain. This species is endemic to Koolan.

Setobaudinia sp. (new species, *fide* V. Kessner). Two (live) were found under sandstone rocks in vine thicket V2 (Feb. 1993).

Kimboraga yampensis Solem. The type locality is a house garden on Koolan Island (WAM 604.80). The original specimens were collected in July 1967 by J. Milton and J. Bannister. In February 1993, one dead shell was found on the patio of a house in town, and a live specimen was taken from a pile of sandstone rocks in vine thicket V2.

Kimboraga koolanensis (Iredale). Known only from four very worn and bleached specimens from Koolan Island held by American museums (Holotype: AM C.64873, Koolan Island). The

Table 2 Occurrence of earthworms on Koolan Island.

Site	Density (m ⁻²)	Abundance ^a Biomass (g m ⁻²)	Occurrence ^b	Species recorded
Vine Thickets				
V1	52.5+/-20.6	9.5+/-6.5	3/4	<i>Diplotrema</i> sp. "koolan2"
V2	18.2+/-10.6	5.1+/-3.2	2/4	<i>Diplotrema</i> sp. "koolan1"
Total:	35.4+/-12.5	7.3+/-3.5	5/8	
Savanna Woodlands				
S1	0	0	0/5	None found
S2	5.0+/-5.0	1.0+/-1.0	1/4	<i>Diplotrema</i> sp. ^c
Total:	2.2+/-2.2	0.4+/-0.4	1/9	
Creek				
T1	0	0	0/3	None found
Town Gardens				
T2	22.5+/-14.9	1.2+/-0.8	2/8	<i>Dichogaster bolau</i>

^a Mean +/- standard error (number of quadrats sampled).
^b Number of quadrats with worms / number of quadrats sampled.
^c Too sexually immature to be placed taxonomically.

collector and date of collection are unknown. Solem (1985) commented that the species should never have been described because "The available material is so badly worn that reference to a genus with any degree of certainty is impossible. ... The large number of whorls, reflected lip, lack of body whorl inflation and lack of body whorl descension also suggest it is not a *Kimboraga*."

Veronicellidae

Laevicaulis alte (Ferussac). Three specimens of this introduced slug were taken from the garden of "house No. 90" in town.

Scorpions

Scorpionidae

Urodacus koolanensis Koch. Koolan is the type locality of this endemic Kimberley scorpion. It was collected on Koolan by O. Milton in September 1966 (WAM 68/487).

Buthidae

Lychas alexandrinus Hirst was collected by O. Milton in September 1969 (WAM 73/590). It is widely distributed in arid and semi-arid areas of Australia.

Centipedes

Scolopendridae

Scolopendra morsitans (Linnaeus). A centipede with a world-wide distribution that was collected from Koolan in September 1966 (WAM 80/1490).

Spiders

Ctenizidae

Conothele sp. This undescribed trapdoor spider was found in the Koolan Island supermarket in July 1984 (WAM 93/79), and sent to the WA Museum by L.F.

Theraphosidae

Selenocosmia stirlingi Hogg. Collected by P.R. Davis in a house in town in January 1987 (WAM 90/1931). It occurs across northern Australia.

Selenocosmia sp. (WAM 91/290–291).

Tetragnathidae

Nephila edulis (Labillardiere). An Orb-weaver collected by F.C. van Ingen in May 1979 (WAM 92/1987). Elsewhere in the northern Kimberley it is common only in savanna woodland (Main 1991). It occurs in sub-humid and semi-arid areas.

Heteropodidae

Neosparassus sp. This huntsman was collected by O. Milton in July 1967 (WAM 88/954–956).

Isopedella castanea Hirst. Collected by W.H. Butler in June 1965 (WAM 86/660). It occurs only in the Kimberley.

Actinopodidae

Missulena pruinosa Levitt-Gregg. Collected by L.F. in June 1990 (WAM 90/1720). This trapdoor spider occurs elsewhere in the Kimberley and other wetter parts of northern Australia, normally in rainforests.

Missulena sp. Collected by L.F. in July 1984 (WAM 94/947).

Barychelidae

A trapdoor spider belonging to this family was sent to Barbara York Main (Zoology Department, University of Western Australia) by P. Kovalers in February 1973.

Ants

Formicidae

Monomorium destructor (Jerdon). The Singapore Ant was accidentally introduced to Koolan in a cargo container. P.R. Davis, an entomologist with the Western Australian Department of Agriculture, assessed the problem in 1987, and reported to BHP (unpublished) that the species was common only on the eastern edge of town. By 1990 it had become a significant pest throughout the townsite (P. Bellairs, pers. comm.).

Oecophylla smaragdina (Fabricius). P.R. Davis (pers. comm.) observed Green Tree Ants during his 1987 visit.

Butterflies

Hesperiidae

Chaetocneme denitza (Hewitson). Previously known from the sub-humid Northern Territory and east coast of Queensland.

Cephrènes trichopepla (Lower). A Torresian distribution, throughout northern Australia.

Pelopidas lyelli lyelli (Rothschild). Listed as observed, but not collected, by Koch and van Ingen (1969). No specimens were located in the W.A. Museum collection. It has a Torresian distribution, occurring throughout northern Australia.

Papilionidae

Papilio demoleus sthenelus W.S. Macleay. Found throughout mainland Australia.

Papilio canopus canopus Westwood. Listed by Koch and van Ingen (1969), but we were unable to find any voucher specimens in the W.A. Museum collection. Known from the sub-humid Kimberley and Northern Territory. Koolan is at the southern limit of its range.

Graphium eurypylus nyctimus (Waterhouse and Lyell). Known only from Koolan and the sub-humid Northern Territory.

Cressida cressida cassandra (Waterhouse and Lyell). Known from the sub-humid Kimberley and Northern Territory. Koolan is at the southern limit of its range.

Nymphalidae

Euploea core corinna (W.S. Macleay). Koch and van Ingen (1969) listed *E. sylvester pelor*, but the only specimens we have been able to locate in the W. A. Museum are *E. core corinna*, all dated between 1965 and 1967.

Danaus affinis affinis (Fabricius). Occurs throughout the Torresian Zone.

Danaus hamatus hamatus (W.S. Macleay). Another pan-Torresian species.

Danaus chrysippus petilea (Stoll). Known throughout mainland Australia.

Hypolimnias bolina nerina (Fabricius). Throughout northern and eastern Australia.

Hypolimnias missipus (Linnaeus). Pan-Torresian.

Polyura pyrrhus sempronius (Fabricius). Found throughout northern, eastern and south-eastern Australia.

Acraea andromacha andromacha (Fabricius). Occurs throughout northern, eastern and south-eastern Australia.

Junonia orithya albicincta Butler. Pan-Torresian.

Junonia villida calybe (Godart). Found throughout Australia.

Vanessa itea (Fabricius). Not listed by Koch and van Ingen (1969), although there is a single Koolan specimen dated December 1964 in the W.A. Museum collection. Previously known only from southern Australia.

Hypocysta adiante antirius Butler. Known from the sub-humid Kimberley and Northern Territory. Koolan is at the southern limit of its range.

Melanitis leda bankia (Fabricius). Pan-Torresian.

Xoïs arctoa arctoa (Fabricius). Occurs throughout the Torresian Zone and along the entire eastern coast of Australia

Pieridae

Delias argenthona fragalactea (Butler). Occurs throughout the sub-humid Kimberley and Northern Territory.

Anapheis java teutonia (Fabricius). Listed by Koch and van Ingen (1969), but we were unable to find any specimens in the W.A. Museum collection. It is found throughout mainland Australia.

Cepora perimale scyllara (W.S. Macleay). Pan-Torresian.

Catopsilia scylla etesia (Hewitson). Common throughout most of the northern half of Australia.

Catopsilia pomona pomona (Fabricius). Common throughout northern and eastern Australia.

Eurema laeta lineata (Miskin). Occurs across northern Australia, north of latitude 16°S.

Eurema herla (W.S. Macleay). Widespread in northern and eastern Australia.

Eurema sana (Butler). Occurs across northern Australia, north of latitude 16°S.

Eurema smilax (Donovan). Found throughout mainland Australia.

Eurema hecabe phoebus (Butler). Common throughout most of the northern half of Australia.

Lycaenidae

Arhopala centaurus asopus Waterhouse and Lyell. Known from the Kimberley and sub-humid Northern Territory. Koolan is at the southern limit of its range.

Zizina labrudus labrudus (Godart). Occurs throughout Australia.

Prosotas ?nora (Waterhouse and Lyell). Listed by Koch and van Ingen (1969); a tentative identification based upon damaged specimens.

Amphibians

Hylidae

Litoria rubella. Seen along wet season creeks where rock bars form temporary waterholes, in garden fish ponds, around the town swimming pool and sometimes inside houses during the wet season. Numerous at the edge of an ephemeral pool in a bulldozer scrape in savanna woodland 0.5 km south-east of town (R115770, Feb. 1993).

Reptiles

Crocodylidae

Crocodylus porosus occurs at the tideline in

mangrove inlets and mudflats around the island.

Gekkonidae

Gehyra australis. Nocturnal. Very common in houses and other buildings. More active during the wet season. L.F. observed up to eight individuals at once on the lounge room wall in her house. Also seen catching insects on roads under and on street lights, especially when flying termites were active. Found under buildings, in cupboards, behind pictures hanging on walls etc during the day. Also observed drinking at a bird nectar feeder, and eating banana and mango in a basket of fruit and honey left for birds (L.F. and N.L., pers. obs.). The W.A. Museum has five records spanning the period 1965 to 1993. The most recent specimen (R115707, Feb. 1993) was on a water tank in savanna woodland overlooking aerodrome at western end of town.

Gehyra nana. Three records. One was under sandstone rocks on sandy soil in the savanna woodland in the island's central plateau north of the mine site (R115772, Feb. 93). The other two were under sandstone rock in an open savanna woodland of eucalypts over *Acacia* shrubs with a low grass understorey (R114449–50, Aug. 1992).

Gehyra occidentalis. Five records spanning the period 1965 to 1992. Two were under sandstone rock in an open savanna woodland of eucalypts over *Acacia* bushes in the Koolan Island townsite (R114451–2, Aug. 1992). Another was on a fig tree in a low open savanna woodland of *Eucalyptus miniata* and *Ficus* over hummock grass in a sandstone valley (R114453, Aug. 1992). One was found on the window frame of a house in the town. (R115714, Feb. 1993).

Heteronotia binoei. Two records in August 1992 (R11419–20). Both were found under rubbish in town. The surrounding vegetation was an open savanna woodland of eucalypts over *Acacia* shrubs on sandstone.

Heteronotia planiceps. Seven records between 1981 and 1993. Two were under rubbish in open savanna woodland of *Eucalyptus miniata* over hummock grass on a sandstone scree-slope (R114447–8, Aug. 1992). One was in eucalypt leaf litter in an open savanna woodland of eucalypts over *Acacia* shrubs on sandstone (R114400, Aug. 1992). Another was "under rubbish" in the townsite (R114463, Aug. 1992). One was found under rocks in vine thicket V1 (R115710, Feb. 1993, see Table 1).

Oedura gracilis. One on sandstone rock (Pky) in an open savanna woodland of *Eucalyptus miniata* over hummock grass (R114396, Aug. 1992).

Oedura obscura. One on a *Calytrix* shrub in a low sandstone valley supporting a low open savanna woodland of *Eucalyptus miniata* over *Ficus* and hummock grass (R114468, Aug. 1992).

Oedura rhombifera. The W.A. Museum has two specimen records from the period 1966–7. Often found under buildings. Two lived in a hollow curtain rod in L.F.'s lounge room. They foraged for insects on the lounge room walls at night. There are no other habitat data.

Pygopodidae

Delma borea. The W.A. Museum received five specimen records between 1966 and the late 1980's. Found under leaf litter in open savanna woodland of eucalypts over *Acacia* on sandstone. In town, they were found on the ground under garden mulch and sheets of tin, and sometimes seen during the day as they crossed the road.

Lialis burtonis. Found in open savanna woodland of eucalypts over *Acacia* shrubs and grasses on sandstone. Seen on roads in town at night. Three colour phases were noted on Koolan: dorsal surface reddish brown, dark greyish brown or light grey; ventral surface salmon, dark brown or light grey respectively. The W.A. Museum has one specimen from Koolan, taken in August 1970..

Agamidae

Diporiphora bennettii. The WAM has fifteen records between 1965 and 1993. The August 1992 record (R114397) was basking on "ironstone" rock (presumably Pky) on a rocky slope supporting savanna woodland of eucalypts over dense *Triodia* and other grasses. Another was under a sandstone rock in savanna woodland on sandy soil in the island's central plateau north of the mine site (R115708, Feb. 93).

Scincidae

Carlia amax. Three records between 1973 and 1992. One was found under rubbish in town and another on eucalypt leaf litter in open savanna woodland of eucalypts over *Acacia* shrubs on sandstone (R114401, 114423, Aug. 1992).

Carlia triacantha. Six records between 1965 and 1983. The species was found on leaf litter among sandstone rocks in vine thickets.

Cryptoblepharus carnabyi. Frequent around houses in town, on pillars and garden rockeries (N.L. pers obs.). One was found running on rocks and leaf litter in vine thicket V2 (R115713, Feb. 1993, see Table 1).

Ctenotus inornatus. Six records between 1970 and 1993. The 12 February 1993 record was collected south-east of the town at site S1 (see Table 1) in

low open savanna woodland of *Eucalyptus* and *Terminalia* over *Triodia* hummock grassland with patches of leaf litter on red clay loam with scattered sandstone (Pky) boulders (R115709).

Cyclodomorphus (= *Omolepida*) *maximus*. Only 10 individuals were seen over 12 years (by N.L.). All were seen in town during the wet season, either crossing the road, as road kills or in gardens. The W.A. Museum has two specimen records from the late 1980's.

Glaphyromorphus (*Sphenomorphus*) *isolepis*. There are three records from Koolan. One was under rubbish in the townsite (R114464, Aug. 1992). Two were found in garden compost in town (R115711 -2, Feb. 1993).

Tiliqua scincoides. Observed at the edge of town in savanna woodland on sandstone, feeding on fallen ripe mangoes in town gardens, and drinking at bird baths (N.L., pers. obs.). Eight young were taken from a female "road kill" (January). The six that were still alive were hand-reared and released by L.F.

Varanidae

Varanus acanthurus. Four records. Three in 1986. The fourth was under sandstone rocks on sandy soil in the savanna woodland in the island's central plateau north of the mine site (R115715, Feb. 93). There are three other records from 1986.

Varanus glebopalma. The most commonly seen monitor on the island. It lived in the savanna woodlands, vine thickets, and in town where it was often seen drinking at bird baths and fish ponds. One was seen killing and eating a Green Tree Snake (*Dendrolaphis punctulatus*). The W.A. Museum has one specimen collected in 1966.

Varanus glauerti. Seen in savanna woodlands at the edge of town and in town gardens (N.L., pers. obs.). A sub-adult was rescued from a "Golden Orb Weaver's" web.

Boidae

Aspidites melanocephalus. During his June 1965 visit, W.H. Butler was shown photographs of several snakes from Koolan. According to his unpublished field notes (lodged in the W.A. Museum), one was of a Black-headed Python.

Morelia childreni. Three records between 1966 and 1982 (R29142, 41506 and 106028). The May 1972 record (R41506) was caught by R.E. Johnstone at night on a road through a savanna woodland of *Eucalyptus miniata* and *Callitris intratropica* on the edge of town.

Liasis olivaceus. The most commonly seen snake on Koolan (L.F. and N.L., pers. obs.). Observed on roads at night and in the savanna woodlands,

especially down gullies near temporary waterholes. Sometimes found in buildings. Often foraged arboreally: seen in eucalypts such as *Eucalyptus miniata*, and twice heard falling to the ground under the Mango tree (*Mangifera indica*) behind Lee Fontanini's house, having caught a flying fox (*Pteropus alecto*). Also preyed on birds drinking at leaking water bores. Prey included Yellow-throated Miner, Double-barred Finch, and domestic pets such as caged birds and Guinea Pigs.

Colubridae

Boiga fusca ornata (= *irregularis*). Observed in savanna woodlands, vine thicket (once), town gardens and at night as it crossed roads. The W.A. Museum has one Koolan specimen, collected in 1967.

Dendrolaphis punctulatus. Found in gardens, inside houses and as it crossed roads at night. Also observed moving through savanna of *Eucalyptus miniata* over hummock grass on sandstone scree, and in vine thicket (N.L., pers. obs.). The W.A. Museum has three records of the Green Tree Snake, spanning the years 1966 to 1981.

Elapidae

Furina ornata. Found on roads, in town gardens and in the savanna woodlands. The four specimens in the W.A. Museum were all collected after 1979.

Acanthophis praelongus. Found in town gardens and in the savanna woodlands. On warm nights they were seen crossing roads and lying on concrete paths. The W.A. Museum holds five Death Adders from Koolan Island. One was received in October 1966 and the other four are dated 8 August 1970.

Oxyuranus scutellatus. The W.A. Museum has three specimens of Tiapan from Koolan, one sub-adult and two adults. The species was first collected in 1984 (R91244) as a road-kill in town. In 1985, an adult was killed by a dog in town (R106029). Two other adults have been found in open savanna woodland of eucalypts over *Acacia* shrubs and grasses on sandstone (R103731, road-kill, late 1980's). All three adults were recorded on particularly hot days (N.L., pers. obs.).

Pseudechis australis. Recorded on roads at night, in town, and in the savanna woodlands of eucalypts, *Callitris*, *Acacia* shrubs and grasses on sandstone surfaces. The WAM's eight "King Brown" specimens from Koolan were recorded between 1966 and 1986. They are small and brownish (L.A. Smith, pers. comm.).

Demansia papuensis melaena. One Greater Black Whipsnake in August 1974 (R47684). There are no habitat data.

Demansia olivacea. The W.A. Museum has five Koolan specimens of the Olive Whipsnake spanning the years 1965 to 1988. It has been observed in the savanna woodlands, and foraging under leaf litter in a town garden.

Typhlopidae

Ramphotyphlops kimberleyensis. One from the townsite (R91044, May 1985). In garden rubbish: a pile of sticks, grass and leaf litter containing many ants.

Ramphotyphlops yampiensis. The only known specimen of this species was collected on Koolan (March 1966, 13 cm long). No habitat data are available (R26839).

Birds

Australian Pelican (*Pelecanus conspicillatus*). Seen once, a single bird, at wharf.

Brown Booby (*Sula leucogaster*). Seen once, marine

Least Frigatebird (*Fregata ariel*). All seasons, common, marine.

Great-billed Heron (*Ardea sumatrana*). Wet season and early dry, scarce, mangroves and coastal mudflats.

White-faced Heron (*Ardea novaehollandiae*). Scarce in dry season, rare in Wet, mangroves and town sewerage outfall.

Eastern Reef Egret (*Egretta sacra*). All seasons (resident), common, all coastal habitats.

Striated Heron (*Butorides striatus*). All seasons (resident), common, mangroves.

Black-necked Stork (*Xenorhynchus asiaticus*). Four seen in 10 years, coastal.

Sacred Ibis (*Threskiornis aethiopicus*). Two seen in 10 years, lawn of school oval.

Straw-necked Ibis (*Threskiornis spinicollis*). Four seen in 10 years, lawn of school oval.

Royal Spoonbill (*Platalea regia*). One seen in 10 years, lawn of school oval.

Black Swan (*Cygnus atratus*). Seen once in 10 years, party of 12, at wharf.

Osprey (*Pandion haliaetus*). All seasons (resident), common, coastal.

Black-shouldered Kite (*Elanus notatus*). Two seen in 10 years, foraging over airstrip.

Black Kite (*Milvus migrans*). Regularly seen in dry season, uncommon, town rubbish dump.

Brahminy Kite (*Haliastur indus*). All seasons (resident), common, foraged in all habitats.

Whistling Kite (*Haliastur sphenurus*). Regularly seen except in mid wet season.

Brown Goshawk (*Accipiter fasciatus*). All seasons (resident), common in woodlands, occasionally seen in mangroves.

White-bellied Sea-Eagle (*Haliaeetus leucogaster*). All seasons (resident), common, coast and town dump.

Wedge-tailed Eagle (*Aquila audax*). All seasons, uncommon, all habitats including town rubbish dump.

Little Eagle (*Hieraaetus morphnoides*). All seasons, uncommon, town and woodlands.

Spotted Harrier (*Circus assimilis*). Seen once in 10 years.

Peregrine Falcon (*Falco peregrinus*). Seen twice in 10 years.

Australian Hobby (*Falco longipennis*). All seasons, uncommon, woodlands and town.

Grey Falcon (*Falco hypoleucos*). Seen once in 10 years, woodland.

Brown Falcon (*Falco berigora*). Uncommon in dry season, scarce in wet season, woodlands.

Australian Kestrel (*Falco cenchroides*). Scarce, usually over open-cut mine.

Brown Quail (*Coturnix australis*). All seasons (resident), common, woodlands and town.

Red-chested Button-quail (*Turnix pyrrhothorax*). Seen once in 10 years, edge of town.

Buff-banded Rail (*Rallus philippensis*). Seen once in 10 years, in town garden.

Baillon's Crake (*Porzana pusilla*). Seen once in 10 years, in brightly lit mine workshop at night.

Bush Thick-knee (*Burhinus magnirostris*). One found dead in town.

Large Sand Plover (*Charadrius leschenaultii*). Seen twice in 10 years, early wet season, coastal mudflat.

Eastern Curlew (*Numenius madagascariensis*). One seen in 10 years, wet season, coastal mudflat.

Whimbrel (*Numenius phaeopus*). All seasons, scarce, coastal mudflats.

Little Curlew (*Numenius minutus*). Late dry season and early wet, scarce, usually on lawn of school oval.

Grey-tailed Tattler (*Tringa brevipes*). Late dry and wet season, scarce, coastal mudflats.

Common Sandpiper (*Tringa hypoleucos*). All seasons, scarce, coastal mudflats and mangroves.

Greenshank (*Tringa nebularia*). One seen in 10 years, wet season, coastal mudflat.

Black-tailed Godwit (*Limosa limosa*). One seen in 10 years, late dry season, coastal mudflat.

- Australian Pratincole (*Stiltia isabella*). Three seen in 10 years, airstrip and road verges.
- Silver Gull (*Larus novaehollandiae*). All seasons, common, town rubbish dump and wharf.
- Caspian Tern (*Hydroprogne caspia*). Uncommon, marine.
- Crested Tern (*Sterna bergii*). Uncommon, marine.
- Rose-crowned Fruit-Dove (*Ptilinopus regina*). One seen in 10 years, in thicket of *Ficus opposita* near powerhouse.
- Peaceful Dove (*Geopelia placida*). All seasons (resident), common, all habitats except coastal mudflat.
- Diamond Dove (*Geopelia cuneata*). One seen in 10 years, wet season, in town.
- Bar-shouldered Dove (*Geopelia humeralis*). All seasons (resident), common, all habitats except coastal mudflat.
- Common Bronzewing (*Phaps chalcoptera*). All seasons (resident), common, all habitats except coastal mudflat.
- Red-tailed Black-Cockatoo (*Calyptorhynchus magnificus*). All seasons (visitor), common, woodlands.
- Little Corella (*Cacatua sanguinea*). All seasons except late wet, common, woodlands.
- Red-collared Lorikeet (*Trichoglossus rubritorquis*). All seasons except mid-dry (May – July), common, woodlands and town where it fed on flowering *Eucalyptus miniata*, then on garden mangos (*Mangifera indica*), then when the mango trees finished flowering, fed on flowering *Eucalyptus confertiflora*.
- Varied Lorikeet (*Psitteuteles versicolor*). Only in late dry season (when the *Eucalyptus miniata* flowered), scarce, woodlands.
- Red-winged Parrot (*Aprosmictus erythropterus*). All seasons (resident), common, all habitats except open coastal mudflats.
- Northern Rosella (*Platycercus venustus*). All seasons (resident), common, all habitats except mangroves and open coastal mudflats.
- Oriental Cuckoo (*Cuculus saturatus*). One seen in 10 years, wet season, in town.
- Pallid Cuckoo (*Cuculus pallidus*). Two seen in 10 years, in town.
- Brush Cuckoo (*Cuculus variolosus*). One seen in 10 years, October, in town.
- Black-eared Cuckoo (*Chrysococcyx osculans*). Three seen in 10 years, in town.
- Horsfield's Bronze-Cuckoo (*Chrysococcyx basalis*). Three seen in 10 years, in town.
- Common Koel (*Eudynamis scolopacea*). One seen in 10 years, wet season (March), in town.
- Pheasant Coucal (*Centropus phasianinus*). All seasons (resident), common, all habitats except coastal mudflats.
- Southern Boobook (*Ninox novaeseelandiae*). All seasons (resident), common, woodlands and town.
- Barking Owl (*Ninox connivens*). Two seen in 10 years, in an African Sausage Tree (*Kigelia pinnata* – introduced) in a town garden.
- Tawny Frogmouth (*Podargus strigoides*). All seasons (resident), common, all habitats except open coastal mudflats.
- Australian Owlet-nightjar (*Aegotheles cristatus*). One seen in 10 years (April), on beach at dusk.
- Fork-tailed Swift (*Apus pacificus*). October to April (associated with clouds during build-up to wet season), common.
- Azure Kingfisher (*Ceyx azurea*). Five seen in 10 years, four in mangroves and one at town swimming pool.
- Blue-winged Kookaburra (*Dacelo leachii*). All seasons, uncommon but rowdy, woodlands and town.
- Red-backed Kingfisher (*Halcyon pyrrhopygia*). Three seen in 10 years, woodlands.
- Sacred Kingfisher (*Halcyon sancta*). All seasons, uncommon, all habitats except open coastal mudflats.
- Rainbow Bee-eater (*Merops ornatus*). Arrived in March and departed in November, common, all habitats except open coastal mudflats.
- Dollarbird (*Eurystomus orientalis*). Five seen in 10 years, vagrant, mainly in town.
- Barn Swallow (*Hirundo rustica*). One party of six seen in 10 years, wet season, over the town.
- Welcome Swallow (*Hirundo neoxena*). One party of three seen, in July 1985, over the town.
- Tree Martin (*Cecropis nigricans*). Mainly dry season, scarce, woodlands.
- Black-faced Cuckoo-shrike (*Coracina novaehollandiae*). Scarce in wet season (January – March) and common in dry, woodlands and town.
- White-bellied Cuckoo-shrike (*Coracina papuensis*). All seasons (resident), common, all habitats except open coastal mudflats.
- White-winged Triller (*Lalage sueurii*). Dry season visitor, uncommon, woodlands.
- Kimberley Flycatcher (*Microeca flavigaster tormenti*). Two seen in 10 years, mangroves.

- Mangrove Golden Whistler (*Pachycephala melanura*). Two seen in 10 years, mangroves.
- Rufous Whistler (*Pachycephala rufiventris*). Scarce, woodlands.
- Sandstone Shrike-thrush (*Colluricincla woodwardi*). All seasons (resident), common, sandstone cliffs.
- Broad-billed Flycatcher (*Myiagra ruficollis*). Four seen in 10 years, mangroves.
- Leadend Flycatcher (*Myiagra rubecula*). All seasons (resident), common, woodlands and edge of mangroves.
- Shining Flycatcher (*Myiagra alecto*). Two seen in 10 years, mangroves.
- Northern Fantail (*Rhipidura rufiventris*). All seasons (resident), common, all habitats except open coastal mudflats.
- Willie Wagtail (*Rhipidura leucophrys*). Arrived in March and departed in October, common, woodlands (including town) and mangroves.
- Lavender-flanked Fairy-wren (*Malurus lamberti rogersi*). All seasons (resident), common, all habitats except coastal.
- Weebill (*Smicrornis brevirostris*). All seasons (resident), common, all habitats except open coastal mudflats.
- Varied Sittella (*Daphoenositta chrysoptera*). Mainly dry season, uncommon, woodlands.
- Silver-crowned Friarbird (*Philemon argenticeps*). All seasons (resident), common, all habitats except open coastal mudflats.
- Little Friarbird (*Philemon citreogularis*). Uncommon, dry season, woodlands (presence tied to *Eucalyptus miniata* flowering).
- Yellow-throated Miner (*Manorina flavigula*). All seasons (resident), common, all habitats except open coastal mudflats.
- White-gaped Honeyeater (*Lichenostomus unicolor*). All seasons (resident), common, all habitats except open coastal mudflats.
- White-throated Honeyeater (*Melithreptus albogularis*). All seasons (resident), common, all habitats except mangroves and open coastal mudflats.
- Brown Honeyeater (*Lichmera indistincta*). All seasons (resident), common, all habitats except open coastal mudflats.
- Rufous-throated Honeyeater (*Conopophila rufogularis*). Uncommon, mainly dry season, woodlands (while *Eucalyptus miniata* was flowering).
- Banded Honeyeater (*Certhionyx pectoralis*). Uncommon, mainly dry season, woodlands (while *Eucalyptus miniata* was flowering).
- Red-headed Honeyeater (*Myzomela erythrocephala*). Three seen in 10 years, mangroves.
- Mistletoebird (*Dicaeum hirundinaceum*). All seasons (resident), common, all habitats except open coastal mudflats.
- Striated Pardalote (*Pardalotus striatus melanocephalus*). All seasons (resident), common, all habitats except mangroves and open coastal mudflats.
- Yellow White-eye (*Zosterops lutea*). All seasons (resident), common, all habitats except open coastal mudflats.
- Double-barred Finch (*Poephila bichenovii*). All seasons (resident), common, all habitats except open coastal mudflats.
- Gouldian Finch (*Erythrura gouldiae*). One seen in 1978, in town garden.
- Yellow Oriole (*Oriolus flavocinctus*). Three seen in 10 years, dry season, town and mangroves.
- Olive-backed Oriole (*Oriolus sagittatus*). Dry season, uncommon, all habitats except open coastal mudflats.
- Spangled Drongo (*Dicrurus hottentottus*). Late dry, scarce, woodlands and town.
- Great Bowerbird (*Chlamydera nuchalis*). All seasons (resident), common, all habitats except open coastal mudflats.
- Australian Magpie-lark (*Grallina cyanoleuca*). Arrive in April and depart in December, common, woodlands and town.
- Black-faced Wood-swallow (*Artamus cinereus melanops*). "One from low woodland" (Smith, Johnstone and Dell 1978)
- White-breasted Woodswallow (*Artamus leucorhynchus*). All seasons (resident), common, all habitats except open coastal mudflats.
- Little Woodswallow (*Artamus minor*). All seasons, uncommon, small parties in woodlands and town.
- Grey Butcherbird (*Cracticus torquatus*). All seasons (resident), common, woodlands and town.
- Pied Butcherbird (*Cracticus nigrogularis*). All seasons (resident), common, woodlands and town.
- Little Crow (*Corvus bennetti*). One flock of 20 seen at town rubbish dump in August 1985.

Mammals

Dasyuridae

Dasyurus hallucatus Gould. Common on Koolan Island. It was reported from the rubbish tips, wharf, mine-site and town, and was often killed on roads during the wet season. First collected

on Koolan in November 1959 (M4481, one of three males). Subsequent specimens include M6050, M7161–3 and M10606. In February 1993 we saw one at the swimming pool in town at dusk, and trapped an adult male in savanna woodland on steep sandstone scree (16°08'40"S, 123°47'35"E).

Muridae

Zyomys argurus (Thomas). The first specimen (M7562) was captured in August 1966. More recent specimens include M18568 (Kitchener 1989) and M24302–3. Seen crossing gravel road at night in open savanna woodland on sandstone scree. Also found in town garden sheds, under bags and nesting in potting mix. A 56.5 gm female with two 9.5 gm young attached to its nipples was found on 8 January 1990.

Pteropodidae

Pteropus alecto Temminck. Collected as a skull (M7848, adult) by O. Milton in 1967. The species has also been seen during the day, roosting in the mangroves south of town, and in *Ficus racemosa* in town. It was common in the savanna woodlands and town in all seasons except the mid-dry (May – July). It fed on flowering *Eucalyptus miniata* from August until November/December when the blossom finished, then on garden mangos (*Mangifera indica*) for a month or so until they finished

fruiting, after which it fed on flowering *Eucalyptus confertiflora* until late April (L.F., pers. obs.). On the nights of 11 and 12 February 1993, one was observed feeding on the flowers of *Eucalyptus cadophora* (Collection Nos: Keighery and Gibson 15 and 95, PERTH) at site T2 in town (Fig. 1).

Macroglossus minimus (Geoffroy). In 1989, one was captured in L.F.'s house in town at the time that her African Sausage Tree was flowering. It was subsequently released. We netted an adult female (not pregnant, not lactating) and an adult male at night on 11 February 1993 in the mangrove low forest south of town (mainly *Sonneratia alba*, *Camptostemon schultzei*, *Ceriops tagal*, *Avicennia marina* and *Rhizophora stylosa*).

Megadermatidae

Macroderma gigas (Dobson). Four specimens from Koolan are held by the W.A. Museum (M19707–10, June 1965). They belong to a series of seven males and four females that W.H. Butler took from their day-roost in "one of the old Japanese tunnels opposite the conveyer and the ore bin" (W.H. Butler, unpublished field notes). These adults were on the south side of the island near the loading jetty, but have subsequently been excavated as part of the ore-body.

Hipposideridae

Hipposideros stenotis Thomas. The W.A. Museum

Table 3 Observed foraging microhabitats of bats from Koolan Island in relation to species flight indices. Values were estimated using the method for live bats described in McKenzie *et al.* (1995). Where live bats were not taken on Koolan, values from adults taken elsewhere in the region have been used (mean +/- standard error).

Island	Foraging Microhabitat*	Aspect Ratio	Wing Loading (g cm ²)	Tip Index
<i>Hipposideros stenotis</i>				
hs1		6.22	0.045	1.48
hs2	closed	5.98	0.039	1.72
M23057 ^a		6.26	0.037	1.86
<i>Nyctophilus arnhemensis</i>				
na3	closed	5.82	0.046	1.33
<i>Vespadalus caurinus</i> ^b (n = 7)				
	edge	6.35 (0.08)	0.040 (0.001)	1.34 (0.03)
<i>Chalinolobus nigrogriseus</i>				
92/1	edge	6.80	0.053	1.16
<i>Chalinolobus gouldii</i> ^c (n = 4)				
	edge	6.67 (0.06)	.063 (0.001)	0.95 (0.02)
<i>Taphozous georgianus</i> ^b (n = 11)				
	open	7.71 (0.05)	0.085 (0.003)	0.90 (0.02)
<i>Saccolaimus flaviventris</i> ^d (n = 1)				
	open	9.09	0.111	1.01

* Categories follow Fenton (1990).
^a Bathurst Island; ^b Kununurra; ^c Barred Creek, near Broome; ^d Mitchell Plateau.

has three specimens from Koolan collected by W.H. Butler. One was caught in the "Japanese tunnels" (M19391, June 1965, adult male). The other two were taken from the "Acacia" exploration shaft at the "end of the island" (M10052-3, Nov. 1968, adult males) (W.H. Butler's unpublished field data). We found a pair roosting in a small, humid sandstone (Pky) cave overlooking the coast at 16°07'10"S, 123°44'30"E (13 Feb. 1993) and another pair roosting in a similar site at 16°07'29"S, 123°43'20"E (14 Feb. 1993). The first cave (1 m high x 3 m diameter) was under an exposed sheet of sandstone in savanna woodland on a gentle slope; the other was an upwardly angled fissure (0.7 m diameter) into a sheer cliff-face supporting hummock grass, *Ficus* and *Calytrix*. One adult male was captured from each pair (field numbers hs1 and hs2). When one of the Koolan specimens was released at night with a bioluminescent tag, its flight was slow, fluttering and within 1 m of the ground. Until it reached the cover of dense understorey shrubs, the bat had considerable difficulty controlling its height and directionality in the windy conditions at the time of its release. The species' ultrasound was recorded both hand-held (inside the darkened house at night) and at the time of release (Table 4). Flight morphology measurements from these Koolan and Bathurst individuals are presented in Table 3.

Hipposideros ater gilberti Johnson. Collected by W.H. Butler in the "Japanese tunnels" in June 1965 (M19390). A dead specimen was found in May 1990, and sent to the W.A. Museum by L.F.

Rhinonictis aurantius (Gray). A series of 7 males and 3 females was taken from their day-roost in the "Japanese tunnels" by W.H. Butler in June 1965 (M7445, 7450-2, 19388-9). He captured another in November 1968 "... at water level, in shaft near loading jetty on south side of island ..." (M10054).

Emballonuridae

Saccolaimus flaviventris (Peters). On 10 Feb. 1993, we recorded the ultrasound calls of this species as it foraged high over the woodland canopy at S1 (Figure 1; Table 4). The calls of this species are audible. In June 1982, one of the authors (N.McK.) collected a specimen (M23038) over a beach on Gibbings Island, just 19 km to the west of Koolan.

Taphozous georgianus Thomas. One was collected in the Koolan townsite in November 1961 (M4897). On 10 Feb. 1993, we recorded the ultrasound calls of this species as it foraged high over the woodland canopy at site S1 (Figure 1). On 14 Feb. 1993, we found two colonies of more than

10 individuals in their day roosts in caves on the northern face of the ridge at the old rubbish tip (16°07'40"S, 123°44'40"E); the three females discerned each had one young clinging to its underside. Additional ultrasound recordings were made in the caves.

Vespertilionidae

Nyctophilus arnhemensis Johnson. An adult male (M34448) was collected on Koolan in June 1990 by L.F. We netted another adult male (field number na3, 11 February 1993) at night in the mangrove low forest south of town (mainly *Sonneratia alba*, *Camptostemon schultzei*, *Ceriops tagal*, *Avicennia marina* and *Rhizophora stylosa*). It was later released with a bioluminescent tag, and flew away between the trees at shrub height, with frequent changes in direction. Ultra-sound was recorded both hand-held and as it flew off (Table 4). Flight morphology measurements are presented in Table 3.

Chalinolobus gouldii (Gray). Ultrasound calls referable to this species were recorded from bats flying at canopy height along the road through savanna woodland at S1 (Figure 1) on 10 February 1993. The *C. gouldii* ultrasound data used for the identification were recorded at Barred Creek near Broome (Table 4).

Chalinolobus nigrogriseus (Gould). A male was collected by W.H. Butler in November 1968 (M10055). We netted an adult male (field number 92/1) over a water tank west of town on the night of 9 February 1993. The surrounding vegetation was savanna woodland. Its ultrasound was recorded at night inside the dark house (Table 4). On 10 February 1993, we recorded the ultrasound calls of this species (Table 4) as it foraged around and under the tree canopies in savanna woodland at S1 (Figure 1). Flight morphology measurements are presented in Table 3.

Vespertilio caurinus (Thomas). First collected on Koolan in October 1963 by I. Crawford (M6012). This bat is common in the island's small caves, drains and culverts. On 10 February 1993, we captured five in their dayroost in a drain under the road at 16°08'00"S, 123°44'45"E: one adult male, one sub-adult and three females. One of the females was carrying two naked young, while a second was pregnant with twins. Three others were captured (with *Hipposideros stenotis*) at their day-roost in the cave at 16°07'10"S, 123°44'30"E (13 Feb. 1993). Three were subsequently released at night with bioluminescent tags, and their ultrasound recorded (Table 4). We recorded ultrasounds typical of this species around a house in the townsite on the night of 12 February 1993, and

as it foraged through the savanna woodland at S1 (Figure 1, Table 4) on the night of 10 February 1993.

Canidae

Canis familiaris Linnaeus. On 14 February 1993, we discovered and photographed fresh dog tracks on the western end of the island. The mine manager, Patrick Warrant, confirmed that a single feral dog appeared on Koolan about 1990.

Bovidae

Capra hircus Linnaeus. W.H. Butler (unpublished

field notes) reported the presence of feral goats in June 1965. The goat population was estimated at 120 in the mid-1980's (by L.F.), after which there were attempts to eradicate them. We found a goat skeleton behind the single men's quarters on the northern edge of the town in February 1993.

Caviidae

Cavia porcellus (Linnaeus). Guinea pigs were brought onto the island as cage pets, but there is no evidence of a feral population.

Table 4 Echolocation parameters for bats from Koolan Island recorded using D140 ultrasound detector (Pettersson Elektronik, Sweden), stored on TDK-MAXG60 Metal Type IV cassette tape using a Sony Walkman WMD6C, and measured by zero crossing analysis.

Code ¹	Situation ²	Number of calls	Average frequency (KHz) ³ CF or FM (min.- max.)	Duration ⁴ (ms)
<i>Hipposideros ater gilberti</i> (FM-CF-FM)				
E	confined	3	160(158-162)	3.2, 5.9, 5.8
<i>Rhinonictes aurantius</i> (FM-CF-FM)				
E	hand-held	44	112.5(112-113)	7.8(5.3-10.5)
E	free flying	24	110.5(110-111)	5.7(4.5-5.9)
<i>Hipposideros stenotis</i> (FM-CF-FM)				
hs2	hand-held	23	102.5(102-103)	18.1(15.4-20.9)
hs1	free flying	32	102.5(102-103)	13.5(10.2-21.1)
<i>Macroderma gigas</i> (st-st-FM, similar shape to the <i>Nyctophilus</i>)				
E	free flying	8	45.5(43.5-46.5)-56(54-59.5)	1.8(1.3-2.3)
E	perch	8	28.5(27.5-31)-36.5(35-38)	1.7(1.3-2.3)
<i>Nyctophilus arnhemensis</i> (st-st-FM)				
na3	free flying	18	42(33-49)-63.6(56-71)	2.1(1.4-3.4)
<i>Vespadalus caurinus</i> (st-FM)				
vc1	free flying	4	59.8(59-61)-66.3(64-66)	3.1(2.3-3.5)
vc2	free flying	9	60.6(58-62)-79.8(62-95)	2.5(2.0-4.5)
vc3	free flying	4	62.5(62-64)-70.7(68-74)	1.9(1.4-2.3)
<i>Chalinolobus nigrogriseus</i> (st-FM)				
92/1	confined	49	39.5'(38-41)-67.5(60-75)	1.61(0.8-2.2)
B	free flying	28	37.0(35.5-38.5)-58.7(38.5-75.5)	6.0(4.0-10.8)
<i>Chalinolobus gouldii</i> (st-FM)				
K	free flying	29	32.3(30.5-34)-47.4(34-71)	6.2(3.8-9.8)
B	free flying	30	31.3(30-33.5)-49.1(36-63)	7.3(3.4-9.8)
<i>Taphozous georgianus</i> (sh-FM)				
K	free flying	18	24.8(24-26)-26.7(26-27)	6.7(4.0-8.5)
<i>Saccolaimus flaviventris</i> (sh-FM)				
M	free flying	6	16.6(16-17)-18.5(18-19.5)	13.0(9.8-15.0)
M	feeding	5	17.4(16-19)-23.6(21-26)	6.5(3.0-8.3)

¹ Specimen code in annotated species list herein, or a recording of an unknown bat from Koolan (K), or recording of a tagged bat at Barred Creek near Broome (B), on Mitchell Plateau (M) or near Kununurra (E).

² Calls recorded either (a) after released at night with a bioluminescent tag or outside of a known roost (= free flying), (b) from bat held in the hand at night (= hand-held), (c) free flying in a confined space such as a cave or room (= confined), or (d) after perching in tree to forage (= perch).

³ CF = of constant frequency section of calls; FM = lowest and highest values of call frequency-time sweep. Call shapes include steep-sweep FM (st-FM), shallow-sweep FM (sh-FM) etc.

⁴ Average (max and min) call duration.

⁵ In sets of one to three calls. Sets are 15 to 80 milliseconds apart, with individual calls inside a set 0.25 to 5 milliseconds apart.

Leporidae

Oryctolagus cuniculus Lilljeborg. European (White)

Rabbits were brought onto Koolan as cage pets. Despite some escapes, there is no evidence of a feral population.

DISCUSSION

Koolan supports a sub-set of the Kimberley fauna. Although macro-invertebrates and vertebrates are incompletely sampled, its bird and snake faunas are surprisingly rich considering the island's small size and restricted range of habitats.

The indigenous earthworms all belonged to the genus *Diploptrema* (Acanthrodriolinae sensu Jamieson 1971) and are new to science. This genus is ubiquitous in rainforest patches elsewhere in the Kimberley where each patch has its own endemic species (McKenzie and Dyne 1991). The earthworm populations in Koolan Island rainforests were equivalent in terms of their density and abundance to those reported from rainforest patches on similar sandstone lithologies elsewhere in the Kimberley (mean \pm s.e. = $35.7 \pm 5.8 \text{ m}^{-2}$, $9.2 \pm 2.0 \text{ g m}^{-2}$, $n = 42$; from Tables 4 and 6 in McKenzie and Dyne 1991).

The Koolan savanna woodland specimen is the first *Diploptrema* recorded outside a rainforest environment in the Kimberley. This reflects the lack of previous attempts to survey earthworms in Kimberley savannas, exacerbated by their presence near the surface only after heavy rains and their relatively low density (Table 2). Unfortunately, the

specimen was so sexually immature that it could not be placed taxonomically in relation to the island's other *Diploptrema*: *D. "koolan1"* and *D. "koolan2"*.

Dichogaster bolau, an introduced earthworm that is cosmopolitan in tropical and subtropical parts of the world, was the only species recorded in the gardens of houses in the town. These lush tropical gardens had been established for up to 20 years, and included many species of broad-leaf trees and shrubs such as Banana palms, Sausage Trees and Frangipani. Most had reticulated watering systems to overcome the annual seven month drought of the dry season. Our failure to find *Diploptrema* in these gardens may have related to the presence of the *D. bolau*. This species was probably introduced with potted garden plants during the 1960's, although a box of earthworms was brought onto the island in the early 1980's (L.F., pers. obs.). Elsewhere in Australia, introduced earthworms are known to displace native species from disturbed soil profiles (Wood 1974, Abbott 1985). *Dichogaster bolau* was not recorded outside the town boundaries.

Only seven species of indigenous land snail have been recorded from Koolan Island. Their phylogenetic affinities are with taxa on the adjacent Kimberley mainland (Solem 1991). Three species are known only from Koolan (*Kimboraga koolanensis*, *Setaubaudinea* sp. and *Amplirhagada astuta*).

In 1988, V. Kessner (pers. comm.) recorded five other non-camaenid species on islands elsewhere in the Buccaneer Archipelago: *Gastrocopta*

Table 5 Syntopic land snail assemblages from other islands in the Buccaneer Archipelago (collected by V. Kessner in 1988).

Species	Cockatoo ¹	"Unnamed" ²	Dunvert ³
Pupillidae			
<i>Nesopupa mooreana</i> Pilsbry	—	X	X
<i>Gastrocopta macrodon</i> Pilsbry	X	X	X
<i>Pupoides pacificus</i> (Pfeiffer)	X	—	—
Subulinidae			
<i>Eremonpeas interioris</i> (Tate)	—	X	X
Helicodiscidae			
<i>Stenopylis coarctata</i> (Moellendorff)	X	—	—
Charopidae			
<i>Discocharopa aperta</i> (Moellendorff)	—	—	X
Helicarionidae			
<i>Westralcystis lissus</i> (E.A. Smith)	X	X	X
Camaenidae			
<i>Torresitrachia bathurstensis</i> (E.A. Smith)	X	X	X
<i>Kimboraga yampensis</i> Solem 1985	X	X	X

¹ 16°05'15"S, 123°35'20"E. Under shady bushes on a steep sandstone (Pky) slope (23 July 1988)

² 16°12'15"S, 123°32'40"E. Vine thicket on a mudstone substrate (26 July 1988).

³ 16°17'45"S, 123°30'50"E. In a small patch of vine thicket on a very steep sandstone scree slope (26 July 1988).

macrodon, *Pupoides pacificus* *Stenopylis coarctata*, *Nesopupa mooreana* and *Discocharopa aperta*. These species are all likely to occur on Koolan because they disperse readily (see Solem and McKenzie 1991) and were found in environments that are well represented on the island (Table 5). For the same reasons, two of the other non-camaenid species that are known from the adjacent mainland might occur on Koolan: *Pumilicopta kessneri* Solem 1989 and *Gastrocopta simplex* Solem 1989 (Pupillidae). In our opinion, a further field survey is needed if a complete listing of the island's non-camaenid land snails is to be obtained.

Six camaenid species (five genera) are known from the Buccaneer Archipelago. Four of these are known to occur on Koolan. Unlike the other land snail families represented in the Kimberley, most camaenid genera show strongly localised patterns of endemism at the species level (Solem 1991). Thus, species such as *Amplirhagada astuta* and the *Setobaudinia* sp. may be endemic to just a few adjacent islands. Others such as *Kimboraga yampensis* are also known from the adjacent mainland (Solem 1991). Data in Table 5 and Solem (1991) suggest that *Torresitrachia bathurstensis*, a representative of the genus *Rhagada* and even a seventh species could also occur on Koolan (NGEN5 NSP50 *vide* A. Solem was collected by V. Kessner from an old termite nest on nearby Margaret Island, 16°09'30"S, 123°34'20"E, 26 July 1988).

We found only one introduced land-dwelling mollusc on Koolan (*Laevicaulis alte*). Although this slug occurs elsewhere in tropical Australia, and ranges as far south as Dampier in Western Australia, it is confined to watered gardens and may not persist on the Island once the town is dismantled.

The list of 34 Koolan butterflies is a sub-set of the Kimberley fauna, although the single specimen of *Vanessa itea* is the first record from the north Kimberley. The collection is dominated by large species. Except in the families Lycaenidae and Hesperidae, the island's butterfly fauna is almost identical to that recorded by Bailey and Richards (1975) from the Prince Regent Nature Reserve, approximately 125km to the north-east. The Prince Regent collections suggest that further collecting would double the list of Koolan Lycaenids and Hesperids. A preliminary examination of the W.A. Museum's moth collection from Koolan suggests a similar sampling bias towards large species.

Although ants are a significant and visible component of the island's fauna, only two species have been identified. One of these, the introduced Singapore Ant, was a significant pest in the townsite (see 'Results'). We know of only one other introduced insect. A "large black cockroach up to 1.5 inches long" was introduced to an adjacent

island (Cockatoo) about 1962, and later to Koolan Island (R. Lind, pers. comm.).

Between 1961 and 1993, 35 reptile and one amphibian species were recorded on Koolan Island. Reptile surveys on Koolan Island have been opportunistic or brief, and sampling bias is apparent from the high proportion of snakes in relation to other reptile species in the list (13 of 34). The list indicates the Torresian affinities of the island's fauna, and provides a good indication of the richness that might be expected on other islands of similar size in the Kimberley. In fact, Koolan is less diverse in terms of its substrates and vegetations than many equivalent or larger islands in the archipelagos and other island groups further north along this coast. It comprises two sandstone formations, but only small areas of mangrove and beach strand vegetation; its few rainforest patches (semi-deciduous vine thickets) are minute (< 0.2 ha), narrow, open canopied even in the wet season, and floristically poor.

A review of the reptiles known from similar habitats on other islands in the Archipelago, and/or the adjacent mainland, suggests that a variety of additional species could occur on Koolan despite its relatively narrow range of habitats (Table 6).

The absence of permanent creeks or pools provides a reasonable explanation for the lack of riparian reptiles such as *Crocodylus johnstoni*, *Elseya dentata*, *Emydura victoriana*, *Liasis fuscus*, *Tropidonophus mairii*, *Gemmatophora gilberti*, *Varanus mertensi* and *V. panoptes*. Similarly, only a single species of amphibian has been collected on Koolan, even though 10 additional species (2 families) are known to occur on the adjacent Yampi Peninsula (Leptodactylidae: *Ranidella bilingua* and *Uperoleia* sp.; Hylidae: *Cyclorana australis*, *Litoria bicolor*, *L. caerulea*, *L. coplandi*, *L. nasuta*, *L. rothii*, *L. splendida* and *L. wotjulumensis*). Two other frog species have been seen on Koolan; both were smaller than *Litoria rubella*, but they have not been identified and no voucher specimens have been taken (L.F., pers. obs.). The lack of red sand surfaces provides a basis for arguing that species such as *Varanus gouldii* and *Ctenotus pantherinus* do not occur on the island.

The other Yampi Formation (Pky) islands in the Buccaneer Archipelago extend in a chain westward from Koolan. Their reptile faunas were sampled during a field survey of the Archipelago in 1982. The relevant collections are lodged in the W.A. Museum. These islands are smaller in area and their known reptiles faunas are subsets of the Koolan fauna. *Pseudechis australis* (Cockatoo, Irvine), *Delma borea* (Cockatoo), *Gehyra occidentalis* (Irvine, Bathurst), *Heteronotia planiceps* (Irvine, Bathurst), *Oedura gracilis* (Irvine, Bathurst), *O. obscura* (Irvine, Bathurst), *Carlia triacantha* (Cockatoo, Irvine, Bathurst), *Ctenotus inornatus*

Table 6 Additional reptiles that might occur inshore or on Koolan Island.

Cheloniidae	Scincidae
<i>Caretta caretta</i>	<i>Carlia munda</i>
<i>Chelonia depressa</i>	<i>C. rufilatus</i>
<i>C. mydas</i>	<i>Cryptoblepharus</i> <i>plagiocephalus</i>
<i>Eretmochelys imbricata</i>	<i>Ctenotus robustus</i>
Dermochelyidae	<i>C. yampiensis</i>
<i>Dermochelys coriacea</i>	<i>Egernia douglasi</i>
Chelidae	<i>Lerista praefrontalis</i>
<i>Chelodina rugosa</i>	<i>Morethia ruficauda</i>
Gekkonidae	<i>Notoscincus ornatus</i>
<i>Crenodactylus ocellatus</i>	<i>N. wotjulum</i>
<i>Diplodactylus conspicillatus</i>	<i>Proablepharus tenuis</i>
<i>D. mcmillani</i>	Varanidae
<i>D. taeniatus</i>	<i>Varanus scalaris</i>
<i>D. stenodactylus</i>	<i>V. tristis</i>
<i>D. ciliaris</i>	Elapidae
<i>Nephruerus asper</i>	<i>Demansia psammophis</i>
<i>Rhynchoedura ornata</i>	<i>Pseudonaja nuchalis</i>
Pygopodidae	<i>Rhinoplocephalus</i> <i>punctatus</i>
<i>Pygopus nigriceps</i>	<i>Vermicella multifasciata</i>
Agamidae	Colubridae
<i>Chlamydosaurus kingii</i>	<i>Cerberus rynchops</i>
<i>Ctenophorus caudicinctus</i>	<i>Fordonia leucobalia</i>
<i>Diporiphora magna</i>	<i>Myron richardsoni</i>
<i>Pogona microlepidota</i>	Hydrophidae
	<i>Hydrelaps darwiniensis</i>
	<i>Hydrophis elegans</i>

(Bathurst), *Glaphyromorphus isolepis* (Cockatoo) and *Varanus glebopalma* (Bathurst).

The 10 years of systematic bird records from Koolan provide a benchmark for assessing the potential bird richness of the many islands that are scattered along the Kimberley coastline. One hundred and sixteen species were recorded during the period, 73 non-passerines and 43 passerines. The Welcome Swallow record extends the known distribution, and Brush Cuckoo and Barking Owl have not previously been recorded on islands in the Kimberley (R.E. Johnstone, pers. comm.).

Absences from the bird list are likely to reflect the absence of suitable habitats rather than incomplete survey of resident species or regular visitors. Koolan is too dry for many Torresian bird species. Its annual average rainfall (960 mm) is significantly less than many islands of similar size further north (South-west Osborne, Katers, D'Arcy etc). This is reflected in the minute size and floristic paucity of its rainforest patches, which may explain the absence or rarity of many "rainforest birds" (*sensu* Johnstone and Burbidge 1991) on the island. Examples include the Torresian Imperial Pigeon, Green-winged Pigeon, Orange-footed Scrubfowl, Little Shrike-thrush, Rufous Fantail, Rufous Owl, Rainbow Pitta, Varied Triller, Green-backed

Flycatcher and Figbird. Some rainforest birds were recorded only in town, probably attracted by the high proportion of broad-leaved tropical plants in the reticulated gardens of the houses: Yellow Oriole and Rose-crowned Fruit-Dove. Low rainfall may also explain the absence of massive scree species such as Black Grass-Wren and White-lined Honeyeater, although White-quilled Rock Pigeons occur in similar sandstone habitat on the adjacent mainland and on Hidden Island, further south in the Buccaneer Archipelago (N.McK., unpubl. data).

The relatively small areas of mangrove around Koolan Island allow an equivalent explanation for the rarity or absence of certain mangrove birds that are common in larger stands that occur in embayments along the mainland coast just a few kilometres away: Chestnut Rail, Little Bronze Cuckoo, Mangrove Kingfisher and Mangrove Robin were not recorded, while the Kimberley Flycatcher, Mangrove Golden Whistler, Broad-billed Flycatcher, Shining Flycatcher and Red-headed Honeyeater were seen on only a few occasions.

The absence of Golden-headed Cisticola and Tawny Grassbirds reflects the rarity of tall grasslands normally found on black-soil plains and flats around swamps on the adjacent mainland. Riparian and fresh-water swamp birds are poorly represented on Koolan because there are no permanent natural creeks or lakes. Some species were seen a few times over the 10 years of observation (e.g., Sacred Ibis, Royal Spoonbill, Baillon's Crake and Buff-banded Rail). Others typical of these habitats on the adjacent mainland were not recorded, including Brolga, White-browed Robin, Red-backed Wren, Bar-breasted Honeyeater, Yellow-tinted Honeyeater, Black-chinned Honeyeater and Chestnut-breasted Mannikan. These species will become more common if the main ore-extraction pit adjacent to the loading jetty becomes a fresh-water lake as discussed in Keighery *et al.* (1995).

A number of other land birds are known from the adjacent mainland or other islands along the coast (Smith *et al.* 1978): Spotted Nightjar, Letter-winged Kite, Black-breasted Buzzard, Collared Sparrowhawk, Grey Shrike-Thrush, Jacky Winter, Restless Flycatcher, Black-tailed Treecreeper, Singing Bushlark, Fairy Martin, Grey-crowned Babbler, Singing Honeyeater, Red-browed Pardalote, Zebra Finch, Star Finch, Masked Woodswallow, Magpie and Torresian Crow. The reason for their absence from the Koolan list is unclear. They may eventually be recorded there; a third of the birds listed from Koolan were encountered three times or less over the 10 year period of observation.

Of the four mammals introduced, only goats appear to have survived. The fourteen indigenous

mammals known from Koolan Island comprise one dasyurid, one rodent and 12 bat species. They are a biased sub-set of the Torresian mammal fauna found on the adjacent mainland.

Considering the extent, intensity and duration of human activity on the island, and the number of natural historians that have searched for ground-dwelling mammals there since 1965, the list may be complete. A field survey in 1983 found only three such species on the largest of the other islands in the Archipelago (Hidden Island, 2003 ha; *Peradorcas concinna*, *Dasyurus hallucatus* and *Mesembriomys macrurus*), two on Long (1380 ha; *Peradorcas concinna* and *Rattus* sp.), and only one species on smaller islands such as Irvine (940, *Zyomys woodwardii*), Bathurst (580, *Zyomys woodwardii*), and Margaret (270, *Mesembriomys macrurus*). The voucher specimens from this survey are lodged in the WA Museum (M23001–23059, M23150–23167).

In contrast to its non-volant mammals, Koolan is rich in bats, especially cave-dwelling species (*Taphozous georgianus*, *Hipposideros ater gilberti*, *H. stenotis*, *Rhinonictis aurantius*, *Macroderma gigas* and *Vespadalus caurinus*). Even so, future surveys will probably reveal additional species because *Miniopterus schreibersii* and *Pteropus scapulatus* are known from nearby islands (Gibbings and King Hall respectively), and other species occur in adjacent areas of the mainland: *Chaerephon jobensis*, *Vespadalus douglasi*, *Pipistrellus westralis*, *Scotorepens sanborni*, *Myotis adversus* and *N. geoffroyi pallescens* (McKenzie and Rolfe 1986).

Little is known about the natural history of *Hipposideros stenotis* in the Kimberley. The sites and small colony-sizes we recorded on Koolan are consistent with previous observations (Kitchener *et al.* 1981, Hall 1983), including a June 1982 record from Bathurst Island (16°03'S, 123°02'E), 15 km west of Koolan, where a female (M 23057) was taken from a pair found in a small sandstone (Pky) cave overlooking the coast.

Our data show that animal-eating bats that forage in the island's open microhabitats have higher wing loadings and aspect ratios, but lower tip indices, than bats of more obstructed air-spaces (Table 3). These attributes relate to flight speed, energy-cost of flight and manoeuvrability, respectively (Norberg and Rayner 1987). Non-parametric ranked correlation analysis revealed a strong correlation between mean "wing loading" and "lowest frequency" in free-flight (Kendall Tau = -1.0, $P = 0.014$), and a significant correlation between mean "aspect ratio" and "lowest frequency" in free-flight (Kendall Tau = -0.8, $P = 0.05$), for the five bats we recorded foraging in "edge" and "open" microhabitats on Koolan (Tables 3 and 4). Such relationships are well documented from work on bat communities elsewhere (e.g. Aldridge 1987, Fullard *et al.* 1991,

McKenzie *et al.* 1995). The data presented in Table 4 suggest that the microbats known from the island can be readily distinguished in terms of the average lowest frequency of their ultra-sounds, and will facilitate future survey work.

The bias towards large land snails and butterflies, snakes and cave-dwelling bats in the Koolan Island fauna lists is a sampling artefact. Nevertheless, the richness of these groups indicates that the numerous rugged sandstone islands along this tropical, sub-humid coastline support much richer faunas than were revealed by the brief surveys carried out to date (e.g., Burbidge and McKenzie 1978).

ACKNOWLEDGEMENTS

We thank Patrick Warrand (Broken Hill Pty Ltd) for arranging accommodation and transportation during our field work, DEST for assistance with funding under National Rainforest Conservation Program, and Peter Agnew (ICI) for his assistance in locating the cave at 16°07'10"S, 123°44'30"E. We also thank Norah Cooper, Mark Cowan, Mark Salotti, Mark Harvey, Terry Houston, Darryl Kitchener, Ron Johnstone and Laurie Smith for access to W.A. Museum collections. Barbara York Main provided advice on spider determinations and contributed data from her records. Mike Lyons drafted Figure 1. Ron Johnstone and the two referees provided helpful comments on the manuscript.

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Revision of the Australian wasp genus *Macrothynnus* Turner (Hymenoptera: Tiphiidae: Thynninae)

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Abstract – The thynnine genus *Macrothynnus* is revised. Both *M. insignis* (Smith) and *M. simillimus* (Smith) are redescribed together with two new species, *M. mustus* and *M. watherooensis*. *M. molitor* (Smith) is removed from synonymy with *M. simillimus* and *M. ioleius* Montet is synonymised with *Onchorhinothynnus xanthospilus* (Shuckard).

INTRODUCTION

Macrothynnus was erected as a subgenus of *Thynnus* Fabricius by Turner in 1908. Five species were included but only *T. insignis* Smith and *T. simillimus* Smith (type species) were retained when the subgenus was raised to generic rank (Turner 1910). There has been no subsequent work published on this genus.

Terminology follows Turner (1908) and Snodgrass (1941). Abbreviations: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, CSIRO, Canberra; BCRI, Biological & Chemical Research Institute, N.S.W. Agriculture, Rydalmere; UCD, University of California, Davis; NTM, Northern Territory Museum, Darwin; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth; T1–7, metasomal tergites 1–7; S1–6, metasomal sternites 1–6.

SYSTEMATICS

Genus *Macrothynnus* Turner

Thynnus (*Macrothynnus*) Turner, 1908: 194; Turner, 1910: 44; Given, 1954: 47; Salter, 1954: 302.

Type species

Thynnus (*Macrothynnus*) *simillimus* Smith, by original designation.

Remarks

Although some of the diagnostic characters used by Turner (1908, 1910) are of dubious diagnostic value (Salter, 1958), the genus can be recognised in the males by an epipygium (tergite 7) which is produced into a small subapical plate and which is longitudinally carinate dorsally and transversely carinate posteriorly (Figure 1), and the absence of spines on sternite 6. It is distinguished from

Zaspilothynnus by the absence of spines on sternite 6, from *Guerinius* by the presence of epipygial (tergite 7) carinae, and *Hemithynnus* and *Megalothynnus* by the presence of a subapical plate. In the females, tergite 2 (Figure 2) is transversely carinate and the pygidium (tergite 6) is subovoid with an almost flat posterior surface which is transversely carinate dorsally becoming longitudinally carinate ventrally and medially, and which is at most slightly excavate dorsally. These character states distinguish females from *Zaspilothynnus* and *Guerinius* which have the pygidium strongly excavate laterally, *Hemithynnus* which has the pygidium laterally spined, *Onchorhinothynnus* which lacks transverse pygidial carinae (apart from a single marginal carina) dorsally, and *Megalothynnus* which lacks continuous transverse carinae on the second tergite.

Key to the species of *Macrothynnus* Turner

(Note The male of *M. molitor* and female of *M. simillimus* are unknown.)

1. Macropterous (males).....2
Apterous (females).....5
2. Antennal prominence, scape, posterior margin of pronotum and legs orange; tergites almost impunctate with indistinct and irregular black marks anteriorly (which may be obscured by the preceding tergite) [WA].....*insignis*
Antennal prominence, scape, pronotum and legs black; tergites finely and closely punctate, without black marks.....3
3. T1 tuberculate medially above anterior truncation.....4
T1 not tuberculate [ACT, NSW]
.....*simillimus*

4. Vertex with small reddish orange mark behind eye; body length > 29 mm; parameres long, narrow and apically truncate (Figure 5) [WA, SA].....*mustus* sp.nov.
Vertex with small reddish orange mark at summit of eye; body length < 28 mm; parameres short, broad and apically rounded (Figures 6) [WA].....*watheroensis* sp.nov.
5. Head, legs and body extensively marked with orange.....*insignis*
Head, legs and mesosoma dark brown to black.....6
6. T1 transversely multicarinate apically; pygidium (T6) as in Figure 8.....*molitor*
T1 not transversely multicarinate apically; pygidium otherwise.....7
7. Pleurites and anterior margin of tergites yellow; pygidium narrowed medially (Figure 9).....*mustus* sp.nov.
Head and body dark brown to black, concolorous; pygidium not narrowed medially (Figure 10).....*watheroensis* sp.nov.

Macrothynnus simillimus (Smith)

Figure 3

Thynnus simillimus Smith, 1859: 15.

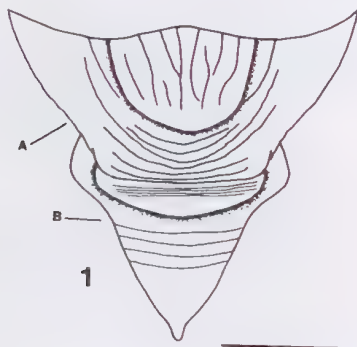
Thynnus (*Macrothynnus*) *simillimus* Smith: Turner, 1908: 194.

Macrothynnus simillimus (Smith): Turner, 1910: 45;
Given, 1954: 47; Salter, 1954: 302.

Material Examined

Holotype

♂, New South Wales, Australia (BMNH 15.144).



Other material

Australia: New South Wales: 1♂, Sydney, W.W. Froggatt (ANIC); 1♂, nr Sydney, Oct.–Nov. 1906 (SAM); **Australian Capital Territory:** 1♂, Jervis Bay, 18 Sept. 1951, S.J. Paramanov (ANIC).

Diagnosis

Large elongate black wasps with the clypeus yellow and metasoma reddish orange in the male. The male is distinguished by the parameres (Figure 3) which are strongly curved and narrowed apically, and by the combination of tergites finely and closely punctate and T1 not tuberculate. It is the only species known from eastern Australia.

Description Male

Measurements

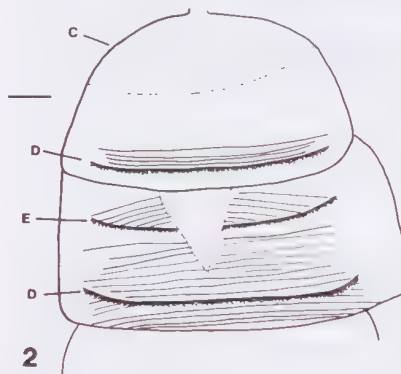
Body: 29–32 mm; fore wing: 23–25 mm; hind wing: 17–18 mm.

Colour

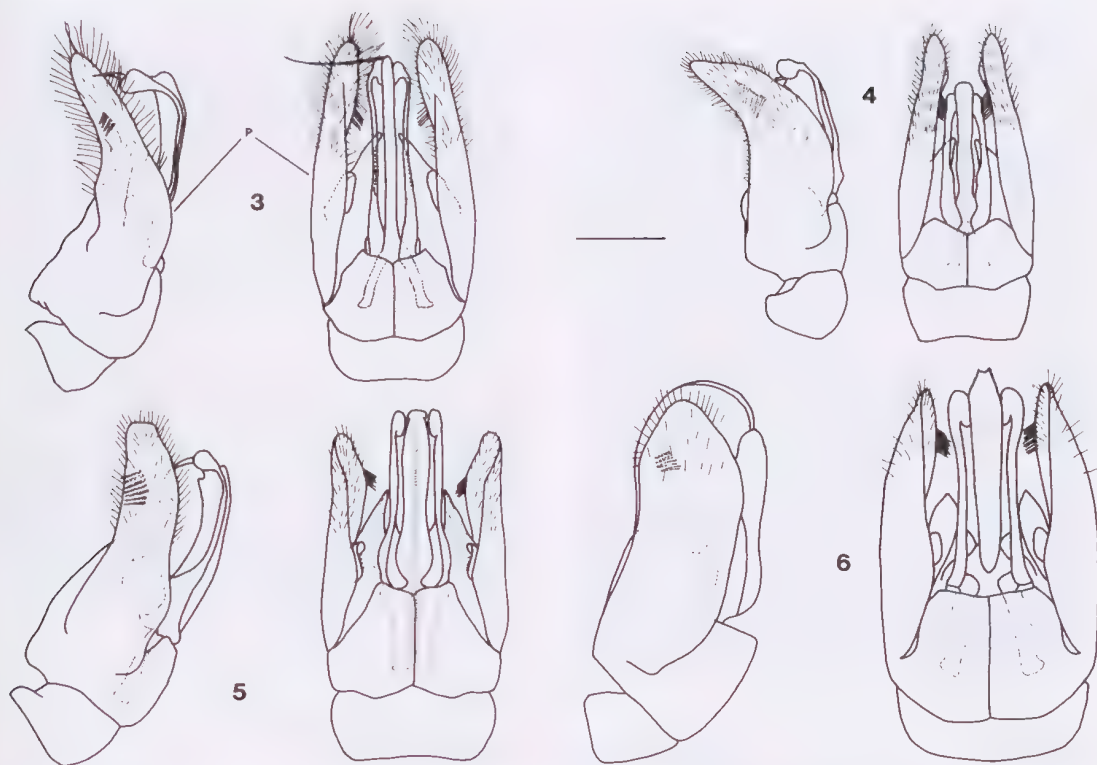
Black; mandibles (except apex) and clypeus yellow; small spot behind eye and metasoma (except base of S1) reddish orange. Wings smoky brown; veins brown or black. Setae white.

Structural features

Clypeus truncate with rugose curved carinae; frons and vertex rugosely punctate; gena finely and rugosely punctate; antennal prominence broadly U-shaped, raised and carinate above antennal insertions; pronotum finely and closely punctate, anterior margin raised, not produced laterally; mesoscutum finely and rugosely punctate; mesoscutellum closely to almost rugosely punctate; metanotum closely to almost rugosely punctate; propodeum oblique without dorsal surface, rugosely punctate, densely covered with long curly setae; mesopleura, prosternum and coxae finely



Figures 1–2 *Macrothynnus* spp.: 1, *M. watheroensis* sp.nov., male, apex of metasoma, dorsal view; 2, *M. molitor* (Smith), female, T1–2. A: T7; B: S8; C: T1; D: preapical carinae; E: basal carina of T2. Scales: 1 mm.



Figures 3–6 *Macrothynnus* spp., male genitalia, lateral and dorsal views: 3, *M. similimus* (Smith); 4, *M. insignis* (Smith); 5, *M. mustus* sp.nov.; 6, *M. watherooensis* sp.nov. P: paramere. Scale: 1 mm.

and closely punctate; fore coxae almost flat; metasoma conical, polished; tergites finely and closely punctate; T1 vertically truncate anteriorly, not tuberculate above anterior truncation; sternites closely punctate; S1 broadly medially raised, obliquely truncate posteriorly; hypopygium (sternite 8) transversely carinate dorsally, broadly rounded apically with apical spine, basal angles produced into small rounded lobes; genitalia as in Figure 3, parameres strongly curved and narrowed.

Female

Unknown.

Distribution

Eastern New South Wales.

Remarks

Turner (1908) synonymised *M. molitor* with *M. similimus* without explanation. This is surprising since the holotypes are of different sexes, and were collected at an unknown locality in South Australia, and Sydney respectively. For these reasons, the absence of sufficient specimens, and a lack of evidence to support this synonymy, *M. molitor*

cannot be considered to be a synonym of *M. similimus*.

The holotypes of both species do not bear locality data labels, despite the locations given in Smith's original descriptions. Further, the putative holotype of *M. molitor* is only presumed so, and is labelled "believed to be Type of *T. molitor* Sm. RET". Smith's description is not sufficient to recognise this species or specimen.

Macrothynnus insignis (Smith)

Figures 4, 7

Thynnus insignis Smith, 1859: 15.

Thynnus (*Macrothynnus*) *insignis* Smith: Turner, 1908: 195.

Macrothynnus insignis (Smith): Turner, 1910: 45; Given, 1954: 47; Salter, 1954: 302.

Material Examined

Holotype

♂, Swan R. Western Australia, Australia (BMNH 15.146).

Other material

Australia: Western Australia: 1♂, 7 mi. (11.3 km) W of Albany, 4 Oct. 1951, I.F.B. Common (ANIC); 1♂, Arrowsmith Crossing, 1 Sept. 1990, B. and B. Wells (BCRI); 2♂, Jewel Cave, 8 km NW of Augusta, 20 Nov. 1986, G.R. Brown (BCRI); 1♀, Beverley, E.F. du Boulay (SAM); 1♂, 14 mi. (22.5 km) W of Borden, 10 Oct. 1951, I.F.B. Common (ANIC); 1♂, 1♀, Deep Dene, Karridale, 4 Nov. 1962, 21 Feb. 1964, L.M. O'Halloran (ANIC); 1♂, 12 km SE of Dongara, 29.20S, 115.01E, 11 Sept. 1981, D.C.F. Rentz (ANIC); 1♂, 1♀, 10 km S of Eneabba, heathland, in cop, 25 Sept. 1986, J.M. Aldenhoven (BCRI); 1♂, Geraldton, 1917, Clark (ANIC); 1♂, King George Sound (AM); 1♂, Kwinana, 19 Oct. 1987, R. Peakall (BCRI); 1♂, Mt Ragged, 1 Nov. 1977, D.H. Colless (ANIC); 1♂, Nornalup, 3 Dec. 1985, J. Alcock (BCRI); 1♂, Northcliffe, L. Glauert (WAM); 1♂, 1♀, Walpole–Nornalup NP., 3 Dec. 1985, J. Alcock, (NTM); 1♂, 1♀, Crystal Springs, 7 mi. (11.3 km) E of Walpole, 14 Dec. 1970, G.A. Holloway & H. Hughes (AM); 1♂, 1♀, Yallingup, 16 Nov. 1968, N. McFarland (SAM); 2♂, Yallingup Cave, pollinating *Caladenia* aff. *huegelii*, Oct. 1990, R. Bates (BCRI); 1♂, Yallingup, on eucalypt, 22 Dec. 1979, R.M. Bohart (UCD).

Diagnosis

Stout and usually large wasps with areas of orange on at least the head, prothorax, legs and metasoma. Males distinguished from all other species by the presence of this colouration on the posterior margin of the pronotum and legs, and by almost impunctate tergites which are black basally. Females are distinguished from all other species by the presence of yellowish orange on the head and mesosoma.

Description Male*Measurements*

Body: 22–35 mm; fore wing: 16–27 mm; hind wing: 12–20 mm.

Colour

Black; mandibles (except apex), clypeus, antennal prominence above antennal insertions, scape ventrally and apically, orbits of eye (discontinuous dorsally), anterior margin of pronotum laterally, posterior margin of pronotum broadly, tegulae, legs (except coxae and fore trochanters), margins of mesopleural lamellae, tergites and sternites (except basally) orange. Wings suffused with orange; veins orange, brown and black. Setae yellow on head and dorsum of pronotum, otherwise white. Tergites and sternites (except basal and apical segments) semitransparent apically so that black colouration of following segments visible.

Structural features

Clypeus truncate, closely punctate with obscure curved carinae; frons, vertex and gena finely and rugosely punctate; antennal prominence broadly U-shaped, raised and carinate above antennal insertions; pronotum finely and rugosely punctate, anterior margin raised and slightly produced laterally; mesoscutum finely and rugosely punctate laterally, coarsely and rugosely punctate medially; mesoscutellum coarsely and rugosely punctate, obscurely sagittally carinate; metanotum finely and closely punctate; propodeum finely and closely punctate, oblique without dorsal surface, densely covered with long curly setae; mesopleura, prosternum and coxae finely and closely punctate; fore coxae almost flat; metasoma conical, polished; tergites almost impunctate; T1 vertically truncate anteriorly, not tuberculate above anterior truncation; sternites closely punctate; S1 broadly medially raised; hypopygium strongly transversely carinate dorsally, broadly rounded apically with apical spine, basal angles produced into small rounded lobes; genitalia as in Figure 4, parameres strongly curved, tapered apically.

Female*Measurements*

Body: 16–27 mm.

Colour

Orange; flagellum, inside occipital carina, anterior surface of pronotum, prosternum, mesothorax, metathorax, propodeum, base and apex of T1 and T3–5, dorsum of T2, pygidium, S1, S5–6 and variably on base and apex of S2–4 dark brown to black; mandibles and base of coxae brown. Setae white to pale yellow.

Structural features

Head subrectangular, wider than long (1.24:1), narrowed ventrally, dorsal angles broadly rounded; clypeus broadly truncate, sagittally carinate, closely punctate; frons coarsely and sparsely punctate becoming closely punctate ventrally; vertex sparsely punctate; pronotum subrectangular, wider than long (1.85:1), slightly narrowed posteriorly, appearing impunctate but very finely and closely punctate, anterior margin with line of coarse punctures; mesoscutellum closely punctate; propodeum truncate with short dorsal surface, finely and closely punctate overlain with coarse punctures dorsally on truncation, lateral surface impunctate and polished becoming closely punctate dorsally and posteriorly with punctures coarser dorsally; tergites sparsely punctate; T1 truncate with preapical carina strongly defined with punctate line; T2 with 8–9 almost complete transverse carinae between

strongly raised basal and preapical carinae, smooth anterior to basal carina and between apical and preapical carinae; T3–5 with obscure preapical carina delineated by line of punctures; sternites punctate becoming closely punctate laterally, and becoming closely punctate on S4; S5 (Figure 7) longitudinally multicarinate, carinae convergent posterolaterally, deeply and closely punctate basally and laterally; pygidium ovoid, slightly upturned ventrally, transversely carinate dorsally, longitudinally carinate dorsomedially, not excavate laterally.

Distribution

South-western Western Australia.

Remarks

Body length is very variable. Specimens are typically large, but the specimens from Kwinana, Northcliffe and Yallingup Cave are distinctly smaller. No structural differences were found in the genitalia of these smaller specimens.

Macrothynnus molitor (Smith)

Figures 2, 8

Thynnus molitor Smith, 1859: 43.

Material Examined

Holotype

♀, no locality data, (BMNH 15.145).

Diagnosis

Large and stout almost black wasp. Distinguished from all species by presence of numerous transverse carinae on T1 apically (Figure 2).

Description Male

Unknown.

Female

Measurements

Body: 25 mm.

Colour

Dark brown to black. Setae pale brown.

Structural features

Head subrectangular, wider than long (1.12:1), narrowed ventrally, dorsal angles broadly rounded; clypeus broadly truncate, sagittally carinate, impunctate; frons coarsely punctate becoming closely punctate ventrally; vertex sparsely punctate; pronotum subrectangular, wider than long (1.86:1), slightly narrowed posteriorly,

very finely and closely punctate overlain with scattered larger punctures, anterior margin with line of coarse punctures; mesoscutellum very finely and closely punctate overlain with larger punctures; propodeum truncate with short dorsal surface, dorsum very finely and closely punctate overlain with larger punctures, lateral surface very finely and closely punctate and polished becoming closely punctate dorsally, posterior surface finely and very closely punctate overlain with scattered shallow punctures; tergites punctate to sparsely punctate; T1 (Figure 2) truncate with strong preapical carina and numerous smaller transverse carinae anterior to preapical carina; T2 with approximately 11 complete transverse carinae between strongly raised basal and preapical carinae, transversely multicarinate anterior to basal carina and between apical and preapical carinae; T3–5 with obscure preapical carina delineated by line of punctures; sternites closely punctate, impunctate posteromedially; S5 (Figure 8) obliquely multicarinate, deeply and closely punctate basally; pygidium subovoid, slightly upturned ventrally, transversely carinate dorsally, longitudinally carinate dorsomedially, lateral margins slightly sinusoidal.

Distribution

South Australia.

Remarks

This species is known from a single specimen which bears the label "believed to be type of *T. molitor* Sm. RET" in R.E. Turner's hand writing. Although Smith (1859) states that the species comes from South Australia, there are no locality labels on this specimen, and it is therefore possible that it may not be the type of *M. molitor*.

The metasoma of this specimen is damaged: T2 has a triangular pin hole (Figure 2), and the right pleurites, especially on T2 are raised.

Macrothynnus mustus sp. nov.

Figures 5, 9

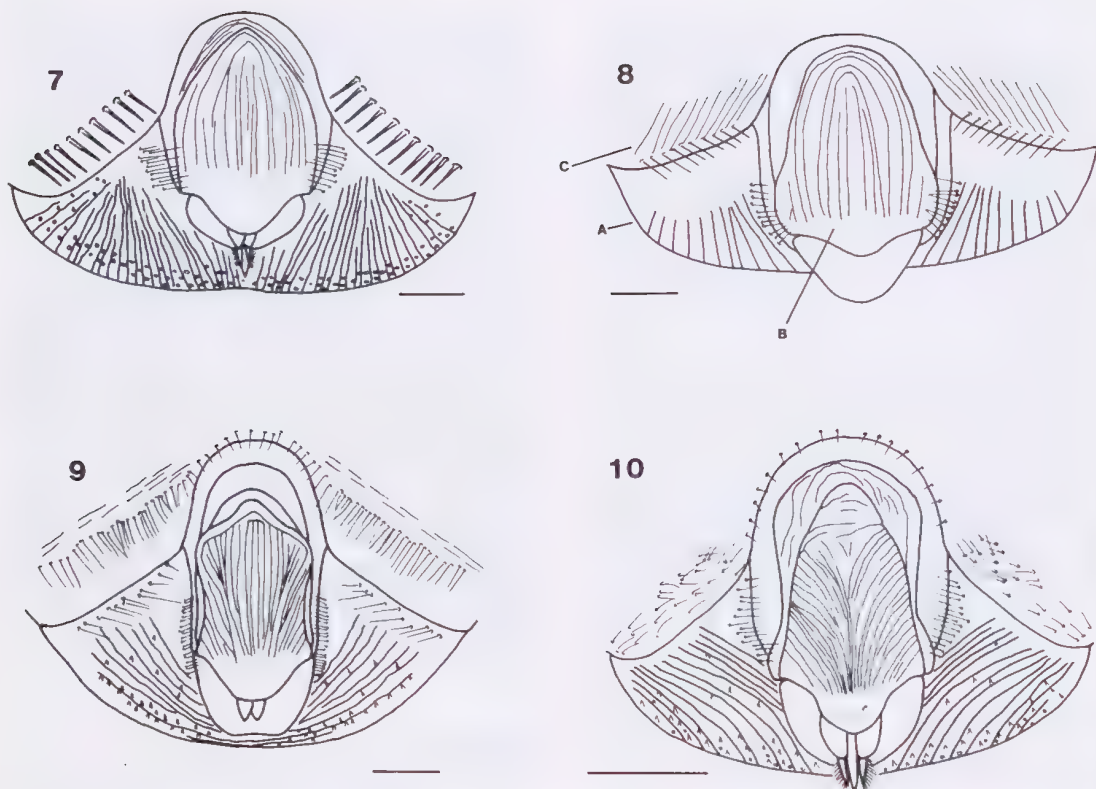
Material Examined

Holotype

♂, Bencubbin, Western Australia: Australia 30.49S, 117.51E, on melaleuca flowers, 9 October 1983, R.P. McMillan (WAM 86–711).

Paratypes

Australia: Western Australia: 1♀, mounted with holotype (WAM 86–712); 1♂, 1♀, same data as holotype (NTM); **South Australia:** 1♂, Ooldea, A.M. Lea (SAM).



Figures 7–10 *Macrothynnus* spp., female, apex of metasoma, posterior view: 7, *M. insignis* (Smith); 8, *M. molitor* (Smith); 9, *M. mustus* sp.nov.; 10, *M. watheroensis* sp.nov. A: S5; B: T6 (pygidium); C: T5. Scales: 1 mm.

Diagnosis

Large elongate black or almost black wasps with the clypeus yellow and the metasoma yellow or reddish orange in the male, and the pleurites and anterior margin of tergites yellow in the female. The male is distinguished by the parameres (Figure 5) which are long, narrow and apically truncate, and is separated from *M. watheroensis* by the presence of a reddish orange spot behind the eye (rather than at the summit of the eye). The female is distinguished from all other species by only the pleurites and anterior margin of the tergites yellow, and the pygidium (Figure 9) narrowed medially.

Description Male

Length

Body: 30–31 mm; fore wing: 26–27 mm; hind wing: 16–17 mm.

Colour

Black; mandibles (except apex), clypeus bright yellow; small obscure spot behind eye and metasoma reddish orange (metasoma rarely yellow). Wings suffused with orange especially on

costal and cubital margins of fore wing becoming infusate distally; veins yellow, brown and black. Setae white becoming pale yellow towards apex of metasoma.

Structural features

Clypeus truncate with rugose curved carinae; frons, vertex and gena finely and rugosely punctate; antennal prominence broadly U-shaped, raised and carinate above antennal insertions; pronotum finely and rugosely punctate, anterior margin raised, not produced laterally; mesoscutum finely and rugosely punctate; mesoscutellum finely and rugosely punctate, sagittally carinate; metanotum finely and closely punctate; propodeum oblique without dorsal surface, closely punctate, densely covered with long curly setae; mesopleura, prosternum and coxae finely and closely punctate; fore coxae almost flat; metasoma conical; tergites finely and closely punctate; T1 vertically truncate anteriorly with sagittal carina on truncation becoming tuberculate dorsally; sternites closely punctate to rugosely punctate; S1 almost flat; hypopygium weakly transversely multicarinate dorsally, subtriangular apically with

apical spine, basal angles produced into small rounded lobes; genitalia as in Figure 5, parameres long, narrow and apically truncate.

Female

Measurements

Body: 25 mm.

Colour

Dark brown to black; pleurites and anterior margin of tergites yellow. Setae white.

Structural features

Head subrectangular, wider than long (1.32:1), narrowed ventrally, dorsal angles broadly rounded; clypeus broadly truncate, sagittally carinate, closely punctate; frons coarsely punctate becoming closely to rugosely punctate ventrally; vertex punctate; pronotum subrectangular, wider than long (1.81:1), slightly narrowed posteriorly, punctate becoming closely punctate anteriorly and laterally; mesoscutellum punctate; propodeum truncate with short dorsal surface, punctate, lateral surface sparsely punctate and polished becoming closely punctate at dorsal and posterior margins; tergites punctate becoming closely punctate on posterior segments; T1 truncate with preapical carina strongly defined with punctate line; T2 with 6 (including preapical) evenly spaced complete transverse carinae, transversely multicarinate anteriorly and between apical and preapical carinae; T3–5 with obscure preapical carina delineated by line of punctures; sternites closely punctate; S5 (Figure 9) transversely and irregularly carinate, rugosely punctate basally; pygidium subovoid, slightly upturned ventrally, transversely carinate dorsally, longitudinally carinate dorsomedially, obliquely carinate ventrolaterally, slightly excavate laterally.

Distribution

Known only from inland southwestern regions of Western Australia and South Australia.

Remarks

The *Ooldea* specimen has the name "A.M. Lea" ruled out with a line through it on the data label. The metasoma of this specimen is yellow and the wings are not darker apically. This suggests that the colour may have faded in this specimen as there are no apparent structural differences in the male genitalia between this and the Bencubbin specimens.

Etymology

The specific name is Latin for new.

Macrothynnus watherooensis sp.nov.

Figures 1, 6, 10

Material Examined

Holotype

♂, Watheroo, Western Australia, Australia 19 October 1985, J. Alcock (NTM I583).

Paratypes

Australia: Western Australia: 10♂, 8♀, same data as holotype (ANIC, NTM, WAM); 4♂, 4♀, Watheroo NP, on *Chamaeleucium uncinatum* blossom, 20 September 1983, 10 October 1984, G.P. Hall (ANIC, NTM, WAM); 1♂, South Perth, 22 October 1903, H.M. Giles (ANIC).

Diagnosis

Large elongate black or almost black wasps with the clypeus yellow and the metasoma reddish orange in the male. The male is distinguished by the parameres (Figure 6) which are short, broad and apically rounded and the presence of a small reddish orange mark at the summit of the eyes. The female is distinguished by the pygidial carinae (Figure 10) which are oblique laterally.

Description Male

Measurements

Body: 12–27 mm; fore wing: 13–23 mm; hind wing: 10–15 mm.

Colour

Black; mandibles (except apex) and clypeus (except oblique submedial mark) yellow; small mark at summit of the eye and metasoma (except base of S1) reddish orange; Wings infusate, fore wing darker distally from level of pterostigma, veins black. Setae white becoming pale yellow towards apex of metasoma.

Structural features

Clypeus truncate with rugose curved carinae; frons, vertex and gena finely and rugosely punctate; antennal prominence broadly U-shaped, raised and carinate above antennal insertions; pronotum finely and rugosely punctate, anterior margin raised, not produced laterally; mesoscutum rugosely punctate; mesoscutellum finely and rugosely punctate, sagittally carinate; metanotum finely and closely punctate; propodeum oblique without dorsal surface, closely punctate, densely covered with long curly setae; mesopleura, prosternum and coxae finely and closely punctate; fore coxae almost flat; metasoma elongate conical; tergites finely and closely punctate; T1 vertically truncate anteriorly with sagittal carina on truncation becoming tuberculate dorsally; sternites finely and very closely punctate; S1 almost flat; hypopygium (Figure 1) weakly transversely carinate dorsally, subtriangular apically with small apical spine, basal angles produced into small

rounded lobes; genitalia as in Figure 6, parameres short, broad and apically rounded.

Female

Measurements

10–19 mm.

Colour

Dark brown to black. Setae white.

Structural features

Head subrectangular, wider than long (1.16:1), narrowed ventrally, dorsal angles broadly rounded; clypeus truncate, not carinate, closely punctate; frons sparsely punctate becoming coarsely and closely punctate ventromedially; vertex sparsely punctate; pronotum subrectangular, wider than long (1.73:1), slightly narrowed posteriorly, reticulate, very finely and closely punctate, anterior margin with line of coarse punctures; mesoscutellum punctate; propodeum truncate with short dorsal surface, finely and closely punctate, lateral surface impunctate and polished with few punctures dorsally and posteriorly; tergites finely and closely punctate overlain with coarser punctures, becoming sparsely punctate anteriorly on posterior tergites; T1 truncate with preapical carina defined by finely and rugosely punctate band; T2 with 7 (including preapical) evenly spaced complete transverse carinae, smooth anterior to basal carina and between apical and preapical carinae; T3–4 with preapical carina and associated microsculpture as T1 but less well defined; T5 rugosely punctate posterolaterally; sternites punctate becoming closely punctate laterally especially on S3–4; S5 (Figure 10) rugose basally becoming obliquely carinate posteriorly; pygidium subovoid, narrowed and excavate basally, slightly upturned ventrally, transversely carinate dorsally, obliquely carinate laterally becoming longitudinally carinate medially.

Distribution

Known only from the Perth and Watheroo areas of Western Australia.

Etymology

The specific name is derived from the type locality.

EXCLUDED SPECIES

Macrothynnus ioleius Montet, 1922

Macrothynnus ioleius Montet, 1922: 212; Given, 1954: 47; Salter, 1954: 302.

Remarks

This species was described from a single female collected at King George Sound, Western Australia, and held in the Paris Museum. The holotype is identical to several females collected with, or mounted with, the males of *Oncorhinothynnus xanthospilus* (Shuckard, 1841) and is therefore considered to be a synonym of that species. There are no female types of *O. xanthospilus*.

Montet's (1922) description of *Macrothynnus ioleius* is the only published description of the female of *O. xanthospilus*.

DISCUSSION

Macrothynnus is a small but distinct genus. It contains some of the largest Australian thynnines second only to *Megalothynnus* in size, and yet at least two species *M. insignis* and *M. watheroensis*, show atypical size variation in which some specimens are half the body length of others. This size variability is unknown in other Australian genera of the subfamily. Its cause is also unknown, but may result from a wide size range in acceptable host larvae, and may be apparent because of the large size of species in this genus. It may be more apparent in *M. insignis* and *M. watheroensis* due to better representations in collections compared to other species of this genus.

At least one species, *M. insignis*, is associated with limestone deposits, and although not restricted to such areas, this species of *Macrothynnus* at least, may prefer host plants and/or larvae found in calcium carbonate rich soils. *M. insignis* was common at Jewel Cave, but difficult to catch. The large size and therefore rapid flight of this, and other species of *Macrothynnus*, may explain the paucity of specimens in collections.

ACKNOWLEDGEMENTS

I thank the curators of the Institutions mentioned for the loan of the specimens in their care, and particularly Mick Day and Tom Huddleston for the loan of types.

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Manuscript received 23 February 1995; accepted 8 May 1995.

Evaporative water loss and colour change in the Australian desert tree frog *Litoria rubella* (Amphibia: Hylidae)

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Abstract – The desert tree frog, *Litoria rubella*, is a small (2–4 g) frog found in northern Australia. These tree frogs typically rest in a water-conserving posture, and are moderately water-proof. Their evaporative water loss when in the water-conserving posture is reduced to 1.8 mg min^{-1} ($39 \text{ mg g}^{-1} \text{ h}^{-1}$) and resistance increased to 7.3 sec cm^{-1} , compared with tree frogs not in the water-conserving posture (7.6 mg min^{-1} , $173 \text{ mg g}^{-1} \text{ h}^{-1}$, 1.1 sec cm^{-1}). When in the water-conserving posture and exposed to dry air, the tree frogs dramatically change colour from the typical gray, brown or fawn, to a bright white. The toe-web melanophore index decreases from 3.8 for moist frogs, to 2.3 for desiccated frogs. The high skin resistance to evaporation and white colour of tree frogs when exposed to desiccating conditions appear to be important adaptations to reduce evaporative water loss and prevent overheating when basking in direct sunlight.

INTRODUCTION

Many species of Australian tree frogs of the genus *Litoria*, are arboreal and frequently perch in exposed sites on vegetation. The desert tree frog, *Litoria rubella* (Gray 1842) is a small, robust species found throughout northern Australia (Cogger 1992; Tyler *et al.* 1994). It survives in arid areas, generally by sheltering in cracks between rocks, or other habitats that provide protection from wind and solar insolation, such as bore holes and water tanks. However, these tree frogs have been observed to perch in sites exposed to direct solar insolation (A.R. Main, *pers. comm.*).

Perching in locations exposed to wind and solar insolation would potentially subject a small frog, such as *Litoria rubella*, to severe desiccation and high body temperatures. Some of the arboreal Australian *Litoria* species have been reported to have reduced rates of cutaneous evaporative water loss (Withers *et al.* 1984; Buttemer 1990) and this would minimise the potential for desiccation when basking. The objective of this study was initially to examine the rate of cutaneous evaporative water loss for the desert tree frog, but preliminary observations revealed that these tree frogs often blanched in colour to a bright white when exposed to dry air. Desert tree frogs are generally grey, brown or fawn in colour, with a broad dark vertebral band and a black stripe along the side of the head (Cogger 1992; Tyler *et al.* 1994). Consequently, the study was extended to investigate the potential roles of ambient humidity and background colour in controlling skin colour.

MATERIALS AND METHODS

Desert tree frogs were collected from a bore on Mallina Station (26° S , 114° E), in the arid Pilbara region of Western Australia. They were transported to the laboratory in Perth, for study. Body mass was measured to $\pm 1 \text{ mg}$; mass ranged from 1.6 to 4.3 g.

The rate of evaporative water loss was determined for individual *L. rubella* at an ambient air temperature of $22\text{--}24^{\circ} \text{ C}$, using flow-through hygrometry. Compressed air was dried by passage through a column of silica gel, and flowed at a rate of 500 ml min^{-1} through a glass tube containing a frog. The excurrent air was passed through a Western Digital DP1100 dewpoint hygrometer for determination of the water content of the air. The analog voltage output of the hygrometer was monitored at 30 second intervals by a PC, and the dewpoint converted to absolute humidity ($\text{mg H}_2\text{O L}^{-1}$) using the psychrometric equations of Parrish and Putnam (1977). The rate of evaporative water loss (EWL; $\text{mg H}_2\text{O min}^{-1}$) of the frog was calculated from the absolute humidity of the incurrent and excurrent air, and the mass specific evaporative water loss (MSEWL; $\text{mg H}_2\text{O g}^{-1} \text{ h}^{-1}$) was then calculated from the body weight (measured to $\pm 0.001 \text{ g}$). The exposed dorsal surface area of the frog (whether it was or was not in the water-conserving posture) was estimated to be $2/3$ of the total body surface area (see Withers *et al.* 1982a; Buttemer 1990) calculated from body weight by the allometric equation of McClanahan and Baldwin (1969) *i.e.* $\text{cm}^2 = 2/3 \cdot 9.9 \text{ g}^{0.567}$. The

surface-area specific evaporative water loss was calculated and converted to resistance by assuming that the gradient in water vapour density was the difference between the vapour density for air saturated at the ambient temperature and the vapour density of excurrent air. The resistance for frogs not in the water-conserving posture was not recalculated although their exposed surface area would have been higher than that of frogs in the water-conserving posture; this means that their resistance was potentially underestimated by as much as 33% (if all of the skin were exposed). The calculated resistance includes some respiratory water loss, hence the actual cutaneous resistance is slightly lower than the calculated value. No correction was made for the air boundary layer to resistance.

For behavioural observations, eight frogs were placed individually in small plastic containers, either white or black in colour, with a transparent lid. The frogs were transferred to the glass tube, with either humid air or dry air flow, and kept in darkness for about 1 hour. The frogs were then removed from the container, and their colour was noted, and eight chromatophores on the transparent toe webbing of a hind foot were quantified by examination under a dissecting binocular microscope for their chromatophore index (CI; Hogben and Slome 1931).

A dark-background and a light-background adapted frog were sacrificed, and their dorsal skin removed and placed in a diffuse reflectance accessory of a Varian dual-beam spectrophotometer (DMS-80), and the reflectance of the skin determined for wavelengths from 200 to 900 nm.



Figure 1 Light-adapted (right; chromatophore index = 2) and dark-adapted (left; chromatophore index = 4) desert tree frogs, *Litoria rubella*.

RESULTS

The rate of evaporative water loss of desert tree frogs was relatively high, about 6 mg min^{-1} or $120 \text{ mg g}^{-1} \text{ h}^{-1}$, if they did not adopt a water-conserving posture in the hygrometer (Table 1), or were placed on a mesh platform to prevent them from concealing their ventral surface from the dry air stream. The skin resistance to evaporative water loss was about 1.1 sec cm^{-1} for these frogs, which is similar to the resistance of a free water surface (about 1 sec cm^{-1}). In contrast, tree frogs which adopted a water-conserving posture and concealed their ventral surface from the dry air stream, had a considerably lower evaporative water loss (1.2 mg min^{-1} , $26 \text{ mg g}^{-1} \text{ h}^{-1}$) and a higher resistance of 7.3 sec cm^{-1} .

The desert tree frogs were observed to change colour dramatically, varying from bright white to a dark brown/black (Figure 1). The chromatophore index varies from 1 (fully aggregated) to 5 (fully dispersed; see Figure 2), and the index of toe-web melanophores was generally found to reflect the dorsal colour of the frog. The index changed according to the general body colour, from 2 (almost completely aggregated for pale frogs) to 5 (fully dispersed for dark frogs). For frogs kept on a white background, the CI was 2.5 ± 0.3 ($n=9$), which was significantly different ($t_{15} = 4.7$, $P < 0.0002$) from the CI of frogs on a dark background of 3.9 ± 0.2 ($n=9$). For frogs from black or white backgrounds and maintained in the dark, in moist or dry air, the chromatophore index (Table 2) was significantly related (2-factor ANOVA) to whether the air was moist or dry ($P < 0.0005$) but not to the original background colour ($P > 0.80$). Frogs in dry air had lower melanophore indices than frogs in moist air *i.e.*

Table 1 Body mass and rates of evaporative water loss and resistance for the desert tree frog *Litoria rubella*, when not in, and in, the water-conserving posture. Values are mean \pm standard error, with the number of observations (n).

	Not in Water Conserving Posture ($n=8$)	In Water Conserving Posture ($n=11$)
Body mass (g)	3.12 ± 0.23	$2.64 \pm 0.26^{\text{NS}}$
EWL (mg min^{-1})	7.63 ± 1.91	$1.84 \pm 0.14^*$
MSEWL ($\text{mg g}^{-1} \text{ h}^{-1}$)	173.2 ± 31.6	$38.8 \pm 5.9^*$
Resistance (sec cm^{-1})	1.09 ± 0.13	$7.29 \pm 0.58^*$

* Significant difference between posture groups ($P < 0.05$), by Student *t*-test.

^{NS} No significant difference between posture groups ($P > 0.05$), by Student *t*-test.

Table 2 Index for chromatophores in the transparent toe webbing of the desert tree frog *Litoria rubella*, kept in moist or dry air after transfer from black or white backgrounds. Values are mean \pm standard error; $n = 8$ for all groups.

	DARK ²	LIGHT ²
MOIST ¹	3.6 \pm 0.4	3.8 \pm 0.4
DRY ¹	2.6 \pm 0.2	2.3 \pm 0.1

¹ significant difference ($P < 0.0005$) by two-factor ANOVA

² no significant difference ($P > 0.8$) by two-factor ANOVA

their melanophores were more aggregated and the frogs were lighter in colour.

The reflectance of the dorsal skin from a dark-coloured tree frog (toe web chromatophore index = 5) varied considerably over the visible spectrum (Figure 2), but was lower than for the dorsal skin of a light-coloured tree frog (toe web chromatophore index = 2). The mean reflectance for the skin samples, from 400 to 700 nm (visible spectrum), was 18.8% for the dorsal skin of the dark tree frog, and 31.8% for the dorsal skin of the light tree frog.

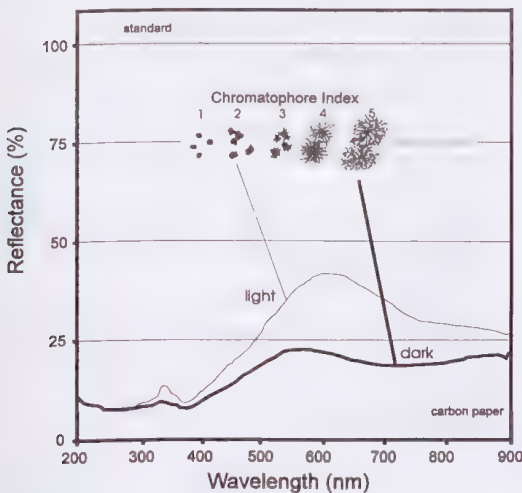


Figure 2 Reflectance of dorsal skin for a light individual of *Litoria rubella* (toe-web chromatophore index = 2) and a dark individual (chromatophore index = 5).

DISCUSSION

Tree frogs, being generally arboreal, are potentially able to bask although there are few specific reports of basking behaviour. *Litoria caerulea* has been reported to bask (Brattstrom 1970) as have *Litoria chloris* (Buttemer 1990) and some other hylids (*H. labiatus* and *Hyla cinerea*;

Valdivieso and Tamsitt 1974; Freed 1980; Snyder and Hammerson 1993); other frogs also bask (Tyler *et al.* 1983; see Hutchison and Dupré 1992). Being exposed to solar insolation and wind in conspicuous basking sites would potentially desiccate and overheat frogs, particularly smaller species such as *Litoria rubella*.

Most amphibians, which evaporate water from their skin as if it were a free water surface, would rapidly dehydrate when basking in exposed, arboreal conditions (see Shoemaker *et al.* 1992; Hutchison and Dupré 1992). Many such frogs adopt a water-conserving posture when exposed to desiccating conditions; the ventral skin is firmly adpressed to the substrate, the limbs are held tightly under the body, and the head is lowered to protect the gular region (see Stille 1958; Pough *et al.* 1983). *Litoria rubella* routinely adopts such a water-conserving posture when perched, and during measurement of evaporative water loss.

A number of arboreal, basking frogs have a reduced rate of evaporative water loss. For example, the Southern African rhacophorid tree frog *Chiromantis xerampelina* has a very low rate of EWL (Loveridge 1970), as does the South American tree frog *Phyllomedusa xerampelina* (Shoemaker *et al.* 1972) and Southern African hyperoliid reed frogs (Withers *et al.* 1982a,b). Consequently, it is not surprising to note that the Australian tree frog *Litoria rubella* has a reduced EWL (Table 1), as do some other *Litoria* spp (Withers *et al.* 1984; Buttemer 1990), at least when they are in the water-conserving posture with the ventral skin concealed. However, the resistance of *Litoria* spp is intermediate (10–40 sec cm⁻¹) between that of typical anuran amphibians (≈ 1) and the “water-proof” frogs (≥ 100). When *L. rubella* were not in a water-conserving posture, their skin resistance to evaporative water loss was only about 1.6 sec cm⁻¹, which is similar to that expected for “non-waterproof” frogs of this size.

Basking in exposed sites presumably elevates body temperature, which confers thermoregulatory advantages (see Hutchison and Dupré 1992). A number of basking frogs (which have a reduced rate of evaporative water loss) blanch to a pale or white colour when basking, presumably to reduce the absorption of incident solar radiation and prevent overheating. The tree frogs *Chiromantis xerampelina* and *Hyperolius* spp are bright white when basking in sunlight (Stewart 1967; Passmore and Carruthers 1979; Kobelt and Linsenmair 1986; Shoemaker *et al.* 1989). The canyon frog *Hyla arenicolor* blanches when basking at high ambient temperature (Snyder and Hammerson 1993). The tree frog *Hyla cinerea* blanches at high ambient temperature (King *et al.* 1994). *Litoria chloris* basks, after feeding (Buttemer 1990). *L. rubella* also basks in sites exposed to solar insolation, and blanches to

a bright white colour (A.R. Main, pers. comm.). The light skin colour increases cutaneous reflectance and decreases the radiative heat load. For example, dorsal skin reflectance increases from 18.8% for dark *L. rubella* to 31.8 % for light individuals (Figure 2); the effective solar reflectance (corrected for the spectral energy distribution of solar radiation; Bakken *et al.* 1978) is similar, at 19.7% for dark frogs and 34.7% for light frogs, because of the similar spectral pattern in both reflectance and solar energy distribution. This change is similar in pattern to that reported for other light-adapted and dark-adapted frogs (Deanin and Steggerda 1948), but is greater in magnitude.

In many amphibians, skin colour is matched to the background colour by dispersion or aggregation of the dermal and epidermal melanophores (Waring 1963). However, reed frogs (*Hyperolius* spp.) blanch to a bright white colour when exposed to dry air (Withers *et al.* 1982b) regardless of their background colour, although the physiological significance of this is not immediately apparent as colour does not directly influence the EWL. Similarly, the desert tree frog *Litoria rubella*, blanches when exposed to dry air, regardless of previous background colour (Table 2). I suggest that this colour change is a response to basking conditions (exposure to dry air) that results in an adaptive increase in reflectance which is an important response to a related basking condition, exposure to incident solar radiation. Colour change in response to humidity does also occur in other frogs, but the effect is minor compared with background matching and temperature effects (Hogben and Slome 1931; Waring 1963).

ACKNOWLEDGEMENTS

I gratefully acknowledge Professor Bert Main for discussions regarding the desert tree frog, and for allowing me to cite his observations as *pers. comm.* I thank Mr John Dell for the loan of tree frogs for photography. Professor Don Bradshaw provided the field opportunity for collection of tree frogs that formed the basis of this study. The comments of two reviewers are gratefully acknowledged.

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Manuscript received 15 December 1994; accepted 5 May 1995.

Chrysiptera kuiteri, a new species of Damselfish (Pomacentridae) from Indonesia and Sri Lanka

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Abstract – A new species of pomacentrid, *Chrysiptera kuiteri*, is described from three specimens. The first specimen was collected during 1991 off northern Bali, Indonesia. Two additional specimens were captured at north-western Sri Lanka in 1994. It is closely related to *C. tricineta* (Allen and Randall) from the western Pacific. The new species differs, however, by having wider dark bars on the body, mainly white pelvic fins, and 20–22 gill rakers on the first arch (23–26 in *C. tricineta*).

INTRODUCTION

Damselfishes (Pomacentridae) are among the most speciose and conspicuous of all fish groups associated with tropical and subtropical reefs. The family was reviewed by Allen (1991), who recognized 322 species in 28 genera. Since the publication of this work seven additional species have been described (Allen 1992, 1993, 1994; Allen and Adrim 1992; Allen and Smith 1992).

The present paper describes a new species belonging to *Chrysiptera* Swainson as defined by Allen (1991). The genus contains 26 species that range widely in the tropical Indo-west and central Pacific region. They are small (usually less than 70 mm SL), frequently colourful fishes inhabiting coral reefs and adjacent sand-rubble habitats. The new species was first collected at the Indonesian island of Bali in 1991. Additional specimens were obtained more recently by the second author at Sri Lanka.

The methods of counting and measuring are the same as those described by Allen (1972), except that the length of the dorsal and anal spines are measured proximally from the base of the spine rather than from the point where the spine emerges from the scaly sheath. Gill-raker count is a total of upper and lower-limb elements on the first branchial arch. The last dorsal and anal soft ray is split at the base and is counted as a single element. The fraction "1/2" appearing in the scale count above the lateral line refers to a small truncated scale at the base of the dorsal fin.

Counts and proportions appearing in parentheses apply to the paratypes. Proportional measurements expressed in thousandths of the standard length are provided in Table 1. A summary of counts for fin rays, lateral-line scales

and gill rakers on the first arch appears in Table 2. Type specimens have been deposited at the National Aquatic Resources Agency, Colombo, Sri Lanka (NARA); Pusat Penelitian dan Pengembangan Oseanologi, Jakarta, Indonesia (NCIP); and the Western Australian Museum, Perth (WAM).

SYSTEMATICS

Chrysiptera kuiteri sp. nov.

Figure 1; Table 1

Holotype

NCIP 6131, 42.8 mm SL, near shipwreck off Tulamben, NE coast of Bali, Indonesia (approximately 8°18'S, 115°37'E), 20m, hand net, R. Kuitier, October 1991.

Paratypes

NARA (F).0015, 32.6 mm SL, off Kandakuliya, northwest Sri Lanka, (approximately 8°14.7'N, 79°40.3'E), 18.5 m, hand net, A. Rajasuriya, 16 March 1994; WAM P.30827–001, 36.2 mm SL, collected with NARA paratype.

Diagnosis

A species of the pomacentrid genus *Chrysiptera* with the following combination of characters: dorsal rays XIII, 11; anal rays II,12; pectoral rays 17 (17 or 18); gill rakers on first branchial arch 6 or 7 + 14 or 15, total rakers 20–22; tubed lateral-line scales 16–18; colour in life white with three broad black bars, the first through eye, the second at level of spinous dorsal fin, and the third at level of soft dorsal fin; pelvic fins mainly white.



Figure 1 *Chrysiptera kuitieri*, holotype, 42.8 mm SL, Tulamben, Bali.

Table 1 Proportional measurements of type specimens of *Chrysiptera kuitieri* as percentage of the standard length.

Character	Holotype NCIP 6131	Paratype WAM P.30827-001	Paratype NARA (F).0015
Standard length (mm)	39.5	36.2	32.6
Body depth	45.3	39.5	45.6
Body width	18.5	18.5	20.0
Head length	33.2	34.0	39.1
Snout length	7.9	8.6	9.4
Orbit diameter	12.9	13.5	13.5
Interorbital width	8.4	9.7	10.3
Caudal peduncle depth	14.7	14.6	15.3
Caudal peduncle length	11.4	12.2	15.0
Predorsal length	40.0	35.4	42.4
Preanal length	63.1	64.9	75.3
Prepelvic length	36.2	40.1	44.4
Length dorsal fin base	64.7	55.2	65.3
Length anal fin base	29.7	23.8	29.7
Length pectoral fin	29.2	30.4	30.0
Length pelvic fin	35.3	38.7	45.0
Length pelvic spine	19.2	21.3	21.5
Length 1st dorsal spine	7.0	7.5	5.6
Length 2nd dorsal spine	11.7	13.8	11.2
Length 6th dorsal spine	17.3	16.9	17.4
Length longest dorsal ray	23.8	24.9	22.1
Length 1st anal spine	6.3	7.7	7.1
Length 2nd anal spine	15.9	16.6	16.8
Length longest anal ray	25.0	29.0	25.9
Length caudal fin	29.9	35.4	32.9

Description

Dorsal rays XIII,11; anal rays II,12; pectoral rays 17 (17 or 18); gill rakers on first branchial arch 7 + 15 (6 +14), total rakers 22 (20); lateral-line scales with tubes 16 (16–18); vertical scale rows; scales above lateral-line to base of middle dorsal spines 1 1/2; scales below lateral line to anus 9.

Body depth 2.2(2.2–2.5) in standard length; maximum body width 2.5 (2.1–2.3) in depth; head length contained 3.0 (2.6–2.9) in standard length; snout 4.2 (4.0–4.2), eye 2.6 (2.5–2.9), interorbital space 3.9 (3.5–3.8), least depth of caudal peduncle 2.3 (2.3– 2.6), length of caudal peduncle 2.9 (2.6–2.8), all in head length.

Mouth oblique, terminal, the maxillary reaching to a vertical slightly beyond anterior edge of eye; teeth of jaws uniserial, conical in shape, about 32 teeth in lower jaw and 38 in upper; single nasal opening on each side of snout; nostril with a low fleshy rim; preorbital and suborbital relatively narrow, the greatest depth about one-fourth eye diameter, ventral margin smooth; margin of preopercle mainly smooth, but weak denticulations present on lower portion of rear margin of holotype; opercular series smooth except a blunt, flattened spine present on upper edge of opercle, near angle.

Scales of head and body finely ctenoid; preorbital, suborbital, snout tip, lips, chin, and isthmus naked; preopercle with 3 scale rows (2

rows in paratypes), rear margin narrowly naked; dorsal and anal fins with a basal scaly sheath; proximal two-thirds of caudal fin covered by scales; paired fins covered by scales only at base; axillary scale of pelvic fins about two-thirds length of pelvic spine.

Tubed lateral-line scales ending below posterior spines of dorsal fin; pits or pores present on 4 (4–6) scales immediately posterior to last tubed; a series of 9 (8) pored or pitted scales mid-laterally on caudal peduncle to caudal base.

Origin of dorsal fin at level of second tubed scale of lateral line; spines of dorsal fin gradually increasing in length to about sixth spine, remaining spines slightly decreasing in length; membrane between spines slightly incised; first dorsal spine 1.7 (1.9–2.0) in second dorsal spine; second dorsal spine 1.5 (1.2–1.6) in sixth dorsal spine; sixth dorsal spine 1.9 (2.0–2.3) in head; longest soft dorsal ray 1.4 (1.4–1.8) in head; length of dorsal fin base 1.5 (1.5–1.8) in standard length; first anal spine 2.5 (2.1–2.4) in second anal spine; second anal spine 2.1 (2.1–2.3) in head; longest soft anal ray 1.3 (1.2–1.5) in head; base of anal fin 2.2 (2.2–2.3) in base of dorsal fin; caudal fin emarginate with rounded lobes, its length 1.1 (1.0–1.2) in head length; pectoral fin relatively short, just reaching a vertical through origin of anal fin, the longest ray 1.1 (1.1–1.3) in head length; filamentous tips of pelvic fins reaching well beyond origin of anal fin, the longest ray 0.9 in head length.

Colour of holotype in alcohol: overall white to yellow white with three broad black bars as follows: one on head passing through eye, its maximum width 1.7 (1.9) in head length; one at level of spinous dorsal fin, tapered ventrally; one extending to belly, but not encircling body, its maximum width 1.2 (1.4–1.6) in head length; one

just anterior to caudal peduncle covering most of soft dorsal fin and extending onto rear portion of anal fin, its maximum width 1.5 (1.4) in head length; dorsal and anal fins translucent to whitish, except where interrupted by black bars; remaining fins translucent to whitish except inner portion of pelvics slightly dusky. The paratypes have a similar coloration.

Colour in life: overall white with three black bars as described above.

Remarks

This species is closely related to *C. tricineta* (Allen and Randall 1974), which has an apparent anti-tropical distribution in the western Pacific Ocean; it occurs from Samoa to the Coral Sea in the South Pacific and from Taiwan to southern Japan in the North Pacific. Although *C. kuiteri* is presently known only from Sri Lanka and Bali, further collecting in the eastern Indian Ocean will probably reveal a more widespread distribution. Its presence at Bali is not unexpected, as many Indian Ocean "vagrants" have been sighted there (Allen and Kuiter personal observations between 1986–1993).

Colour pattern differences are the main means of separation for these two species. The three black bars of *C. kuiteri* are consistently wider than those of *C. tricineta*. This discrepancy is particularly evident when comparing the pair of bars on the body. The maximum width of the first body bar (below spinous dorsal fin) of *C. kuiteri* is wider than the maximum width of the white interspace between the two body bars, at least dorsally. Conversely, in *C. tricineta* the maximum width of the white interspace is considerably wider than the first body bar. Similarly, the last bar of *C. kuiteri* is much broader than the white area of the caudal peduncle. This bar on *C. tricineta* is about equal in



Figure 2 Underwater photograph of *C. tricineta*, approximately 38 mm SL, Coral Sea.

width to the white area of the caudal peduncle. There is also a difference in the colour of the pelvic fins. These fins are mainly white with only a small amount of duskiness on the innermost portion of *C. kuiteri*, but are mainly black with a white anterior margin in *C. tricineta*. There also appears to be a difference in number of total gill rakers on the first arch, although more specimens of both species are required before this can be substantiated. The gill arches are missing in one of the specimens of *C. kuiteri*, but the other two have counts of 20 and 22. Counts for *C. tricineta* range from 23 to 26.

The habitat of both *C. kuiteri* and *C. tricineta* consists of flat or sloping sand bottoms with sparse coral outcrops in a depth range of about 15–30 m. These areas are subjected to strong currents and underwater visibility is generally good (to 20–30 m). *C. kuiteri* is usually encountered alone or in pairs and hovers a short distance above the substratum. Presumably it feeds on zooplankton. The species is uncommon at both Bali and Sri Lanka. Fewer than five fish were sighted at Bali. In addition to the northwestern site on Sri Lanka, it was also sighted at Trincomalee and Batticaloa on the central east coast.

It is named *kuiteri* in honour of Mr. Rudie H. Kuiter of Melbourne, Australia who collected the holotype. The name also acknowledges Mr. Kuiter's many valuable contributions to our knowledge of tropical reef fishes of the Australian-Indonesian region.

ACKNOWLEDGEMENTS

We thank Mr. Rudie H. Kuiter for collecting the

holotype of this species and allowing us to describe it. He also provided valuable underwater photographs. We also thank the Swedish Agency for Research Cooperation with Developing Countries (SAREC) for helping to fund the second author's field work in Sri Lanka.

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Manuscript received 28 September 1994; accepted 16 May 1995.

Sharks from the Middle–Late Devonian Aztec Siltstone, southern Victoria Land, Antarctica

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Abstract – Shark teeth representing three new taxa are described from the Middle–Late Devonian Aztec Siltstone of southern Victoria Land, Antarctica. *Portalodus bradshawae* gen. et sp. nov. is represented by large diploidont teeth which have a base with a well-produced labial platform. It occurs in the middle to upper sections of the Aztec Siltstone. *Aztecodus harmsenae* gen. et sp. nov. is represented by broad bicuspid teeth, wider than high, with numerous medial crenulations and twin nutritive foramina penetrating the rectangular base. It occurs in the middle sections of the Aztec Siltstone. The teeth of *Anareodus stalei* gen. et sp. nov. are characterised by having a main cusp which is more than twice as high as the second cusp, a small cusplet developed on the outer cutting edge of the main cusp, sometimes with few crenulations developed in the middle of the two cusps, and the base is strongly concave. *Antarctilamna* cf. *prisca* Young, 1982 is also recorded from the middle and upper sections of the Aztec Siltstone above the thelodont horizons and occurring with phyllolepid and *Pambulaspis* in the Cook Mountains section south of Mt Hughes. The chondrichthyan fauna from the Aztec Siltstone now contains at least 5 species, being the most diverse assemblage of Middle Devonian chondrichthyans (based on teeth) from one stratigraphic unit.

INTRODUCTION

Fossil shark remains were first identified in the Devonian Aztec fish fauna of southern Victoria Land in the material collected from moraine at Granite Harbour, near the coast of McMurdo Sound, during the British Antarctic 'Terra Nova' Expedition of 1910–13. Among the fish scales observed in thin section were some which Woodward (1921: 57) described as 'typically Elasmobranch, each large cusp showing a trace of an original pulp cavity'. Many of these scales subsequently turned out to be thelodont scales, whose existence in a fish fauna of Late Devonian aspect was completely unsuspected by Woodward and other early workers. These were recently described as a new species of *Turinia* by Turner and Young (1992). White (1968), who studied the first *in situ* material, collected by B.M. Gunn and G. Warren during the Trans-Antarctic Expedition of 1958 (Gunn and Warren 1962), then found one definitive shark specimen, a single tooth which he described as a new form, *Mcmurdodus featherensis*, placed in a new family *Mcmurdodontidae*. This specimen came from Mt Feather, 18 km due east of the Lashly Range (Figure 1). Young (1982) described a second shark, *Antarctilamna prisca*, based on partially articulated remains which included teeth, scales and fin-spines also provided

the first illustrations of the large diploidont teeth from Portal Mountain recorded by Ritchie (1971) as resembling those of *Xenacanthus* sp. These shark remains form part of a diverse fish fauna from the Aztec Siltstone, including arthrodires (Ritchie 1975; Long in press), antiarchs (Young 1988), acanthodians (Young 1989b), rhipidistians (Young *et al.* 1992), lungfish (Woolfe *et al.* 1990, Young 1991), and an undescribed actinopterygian (Young 1991). The faunal list now stands at 22 named genera and 31 species, including the new forms described here, of which all species and 18 genera are endemic to the region of East Gondwana (Table 1).

The material described herein comes mainly from a new collection of Aztec Siltstone fossils made by J. Long on the joint 1991/92 New Zealand Antarctic Research Program–Australian National Antarctic Research Expedition trip to the Cook Mountains and Skelton Nèvé regions, but also includes shark material previously collected by A. Ritchie and G.C. Young during the Victoria University of Wellington Antarctic Expedition VUWAE 15 (1970/71 season). The new material is sufficient to describe three new genera of Devonian sharks, based on teeth. In addition, information from the new localities in the Cook Mountains extends the known stratigraphic range of

Table 1 Vertebrate faunal list for the Aztec Siltstone, Antarctica.

AGNATHA	<i>Turinia antarctica</i> Turner and Young, 1992
PLACODERMI	
Antiarchi	<i>Bothriolepis antarctica</i> Woodward, 1921 <i>B. alexi</i> Young, 1988 <i>B. askinae</i> Young, 1988 <i>B. barretti</i> Young, 1988 <i>B. karawaka</i> Young, 1988 <i>B. kohni</i> Young, 1988 <i>B. macphersoni</i> Young, 1988 <i>B. mawsoni</i> Young, 1988 <i>B. portalensis</i> Young, 1988 <i>B. vutwae</i> Young, 1988 <i>B. sp. indet</i> 1–13. <i>Pambulaspis antarctica</i> Young, 1989
Arthrodira	<i>Antarctolepis gunni</i> White, 1968 <i>Groenlandaspis antarcticus</i> Ritchie, 1975 <i>Groenlandaspis</i> spp. <i>Boomeraspis goujeti</i> Long, 1995a <i>phlyctaeniids</i> spp.
Phyllolepidia	? <i>Austrophyllolepis</i> sp. <i>phyllolepid</i> indet.
Incertae sedis	<i>Antarctaspis mcmurdoensis</i> White, 1968
CHONDRICHTHYES	<i>Mcmurdodus featherensis</i> White, 1968 <i>Antarctilamna prisca</i> Young, 1982 <i>Anareodus statei</i> gen. et sp. nov. <i>Aztecodus harmsenae</i> gen. et sp. nov. <i>Portalodus bradshawae</i> gen. et sp. nov.
ACANTHODII	<i>Gyracanthides warreni</i> White, 1968 <i>Antarctonchus glacialis</i> White, 1968 <i>Byssacanthoides debenhami</i> Woodward, 1921 <i>Culmacanthus antarctica</i> Young, 1989 <i>Cheiracanthoides</i> sp. (scales). <i>Ischnacanthid</i> gen. indet.
OSTEICHTHYES	
Actinopterygii	<i>palaeoniscoid</i> gen. nov. ?palaeoniscoid indet.
Rhipidistia	<i>Gyroptychius?</i> <i>antarcticus</i> (Woodward) <i>Koharalepis jarviki</i> Young <i>et al.</i> , 1992 <i>Mahalalepis resima</i> Young <i>et al.</i> , 1992 <i>Platyethmoidea antarctica</i> Young <i>et al.</i> , 1992 <i>Vorobjevaia dolonodon</i> Young <i>et al.</i> , 1992 <i>Notorhizodon mackelveyi</i> Young <i>et al.</i> , 1992 <i>porolepiform</i> indet.
Dipnoi	? <i>Eoetenodus</i> sp. <i>Howidipterus</i> sp. ?ctendontid indet.

Antarctilamna prisca. Specimens are lodged in the Western Australian Museum, Perth (prefix WAM), the Australian Museum, Sydney (prefix AMF), and the Commonwealth Palaeontological Collection, Australian Geological Survey Organisation, Canberra (prefix CPC).

LOCALITY INFORMATION

Full details of all fossil fish localities known to that time from the Aztec Siltstone were provided by Young (1988). Information is given below for new localities and previous localities yielding described shark material. Numbers refer to localities 1–24 of Young (1988, figure 3). The regions are dealt with here from south to north.

Cook Mountains

Several new sites were discovered in the Cook Mountains during the 1991/92 field season (Figure 1, left). Shark teeth were recovered from "Gorgon's Head" near Mt Hughes, the same area from where fish were first recorded during the 1988/89 season (Woolfe *et al.* 1990). Other material came from the Fault Bluff sections and at Mt Gudmundson. Stratigraphic sections of the Aztec Siltstone and Beacon Heights Orthoquartzite from these localities were measured by M. Bradshaw and F. Harmsen and are currently being compiled. Figure 2 shows the provisional stratigraphic position of the fish faunas from the Cook Mountains referred to in the text, based on field measurement of stratigraphic sections.

Fault Bluff, "fish hotel" section

This stratigraphic section was measured along a low ridge running north-south outcropping immediately north of Fault Bluff (79°18'S, 157°41'E). The stratigraphic sections were logged by M. Bradshaw and F. Harmsen. A continuous outcrop of Aztec Siltstone approximately 91 m thick is exposed here, although the base of the section is covered by scree. By comparison with the surrounding outcrops, the top of the Beacon Heights Orthoquartzite would sit within 20 m of the base of the section. Several fossil fish bearing horizons were located: site "A", about 45 m above the base, contained isolated impressions of fish plates in hard white orthoquartzite; site "B", about 67 m above the base, has rich accumulations of well-preserved fish remains in a medium-coarse to gritty quartzose sandstone; site "M", about 72 m above the base, is a fine, green siltstone with small fragments of well-sorted fish bone and scale debris; site "Y" about 85 m above the base, has occasional fish plates in quartz sandstone; and site "Z", at the top of the exposure about 88–90 m above the base, is a clean, indurated orthoquartzite rich in fish and plant remains. Lycopod stem axes are here

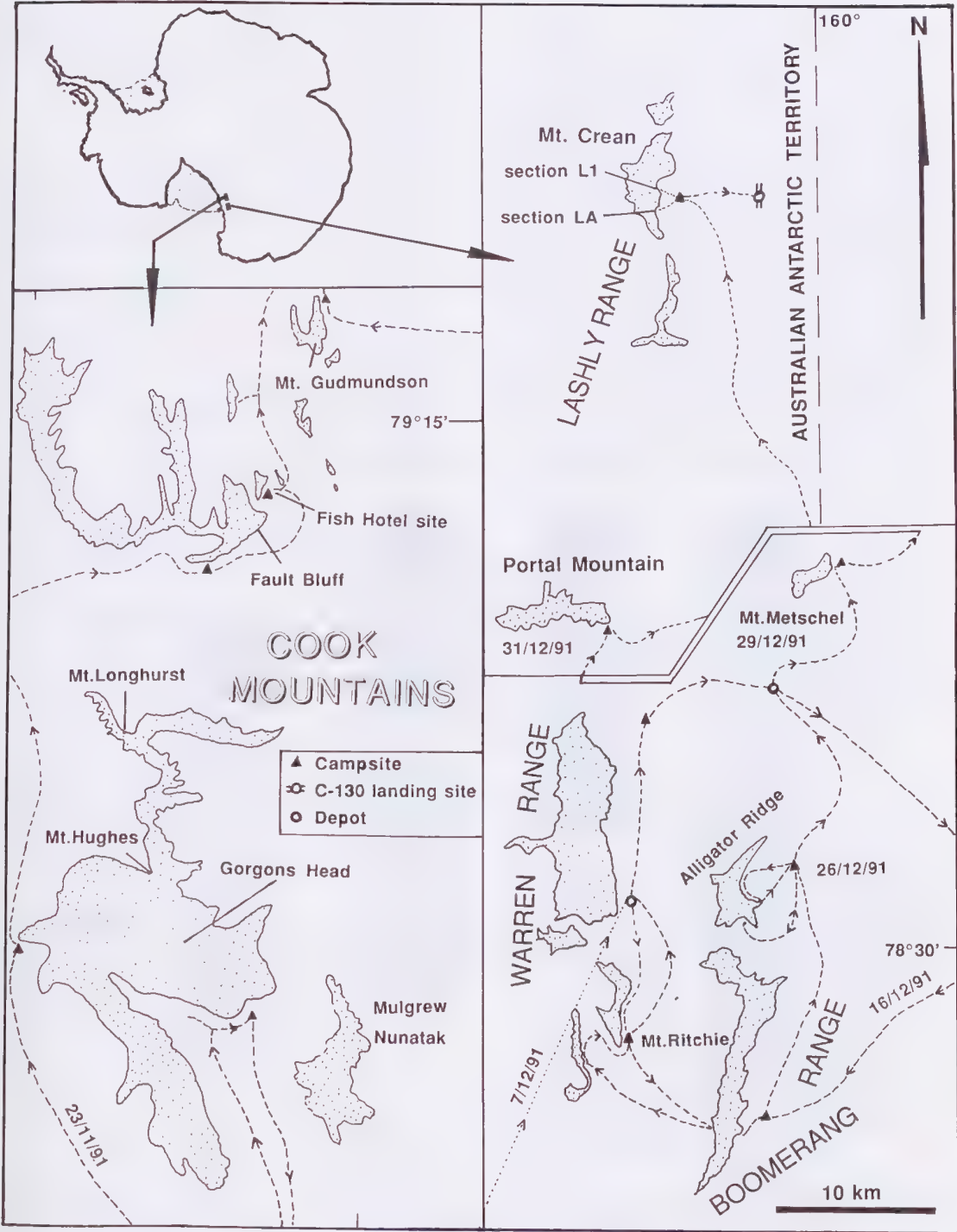


Figure 1 Locality map showing sites visited during the 1991/92 field expedition and localities mentioned in the text.

preserved as 3-D impressions (McLoughlin and Long 1994).

Mt Gudmundson

Approximately 93 m of Aztec Siltstone is exposed here in continuous outcrop, conformably resting upon a thick exposure of Beacon Heights Orthoquartzite and unconformably topped by Darwin Tillite. The stratigraphic section was measured and described by J. Long. At least six different fish bearing horizons identified: site "1", about 2.5 m above the base, with isolated fish plates preserved in black siltstones; site "2", a boulder scree resting on a table of quartzite, about 10 m from base, with rare isolated fish plates; site "3", contains fish fragments about 2 metres higher than previous site in similar lithology; site "4", about 21 m above the base, has isolated fish plates in clean, white medium-grained quartz arenite; site "5" about 54 m above the base, a rich bonebed of fish plates in a pebbly, gritty coarse sandstone-

conglomerate, and site "6", about 90 m above the base in the highest exposure of flat-lying sandstones of the Aztec Siltstone, also a gritty layer with abundant fish bones. Some scree material containing fish fossils in a coarse sandstone was found in between sites 5 and 6 and labelled as site "5.5".

Southern Warren Range

Site 23 (Young 1988)

Section A5, west of Mount Ritchie (70/71). The shark tooth illustrated by Young (1982, plate 88, figure 4) came from the vicinity of section A5 of Askin *et al.* (1971). The precise horizon is uncertain, but was interpreted by Young (1988, text-figure 5) to lie within the range of "*Xenacanthus*" sp. (described herein as *Portalodus bradshawae* gen. et sp. nov.).

Site 24 (Young 1988)

Section A4, Mount Ritchie (70/71). Arthrodire,

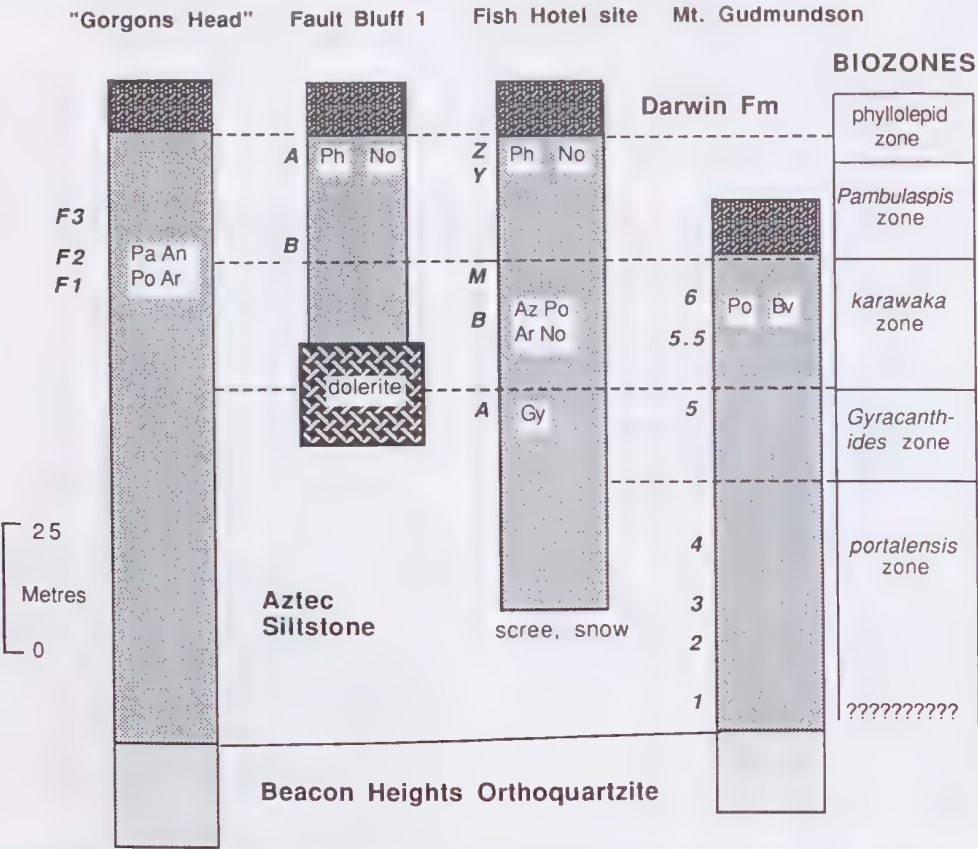


Figure 2 Comparisons of stratigraphic sections from four new localities of Aztec Siltstone fish fauna in the Cook Mountains. Biozonation modified from Young (1988). An, *Antarctilamna prisca*; Ar, *Anareodus* gen. nov., Az, *Aztecodus* gen. nov., Bv, *Bothriolepis vuwae*; Gy, *Gyracanthides warreni*; No, *Notorhizodon mackelveyi*; Pa, *Pambulaspis antarctica*; Ph, phyllolepid common; Po, *Portalodus bradshawae*. Other numbers and abbreviations refer to field localities of fish-bearing horizons.

antiarch and crossopterygian material from the upper fish horizons in this section (units 54 and 62, 187–212 m above base) were described by Ritchie (1975), Young (1988) and Young *et al.* (1992) respectively. Askin *et al.* (1971) also recorded fish remains in the A4 section from lower units 37 and 44 (137 m and 158 m above the underlying Beacon Heights Orthoquartzite), which were not collected in 1970/71. New material from this section collected in 1991/92 comes from a newly discovered site about 120 m above the base in a coarse pink-buff quartzose sandstone, labelled in the field as horizon "M".

Portal Mountain

Site 11 (Young 1988)

Portal Mountain, 68/69 locality. Fish remains were discovered here on the southern face near the end of the eastern ridge from the summit of Portal Mountain by VUWAE 13 in 1968–69. The small collection, including shark teeth, was briefly described by Ritchie (in McKelvey *et al.* 1972). This is section 10 of Barrett and Webb (1973), and the original teeth of *Portalodus bradshawae* gen. et sp. nov. came from unit 17, about 40 m above the lowest exposure of the Aztec Siltstone (base obscured by ice). A fin-spine recorded from here was provisionally referred to *Antarctilamna prisca*, as was another from a higher horizon in the same section (unit 26, 70.8 m above lowest exposure), where more 'xenacanth' (*Portalodus bradshawae* gen. et sp. nov.) teeth were found (Young 1982).

Site 12 (Young 1988)

Portal Mountain, 70/71 locality. The adjacent section P1 of Askin *et al.* (1971) was measured up the eastern face of this outcrop, and shark scales and teeth were referred to *Antarctilamna prisca* by Young (1982).

Portal Mountain, 91/92 locality

New material was collected from the eastern face about 200 m west of locality 11. The specimens came from about 70 m from the base of the Aztec Siltstone in a red mudstone which has lenses of fish bones and scales.

Lashly Range

Site 8 (Young 1988)

Mount Crean. The original *in situ* material from this locality (Gunn and Warren 1962) was described by White (1968). Section L2 of Askin *et al.* (1971; also McPherson 1978) was measured here, and stratigraphic levels for seven collecting sites at this locality (MC 1–7) were discussed by Young (1988: 12,13).

Site 9 (Young 1988)

Lashly Mountains, southeast of Mount Crean. The type locality and horizon for the holotype of *Antarctilamna prisca* Young, 1982, is from about 15 m above the base of the Aztec Siltstone, probably units 8–10 in section L1 of Askin *et al.* (1971).

New locality, third outcrop of Aztec Siltstone southeast of locality 8

This is the type locality for *Aztecodus harmsenae* gen. et sp. nov. This section (field name "LA") is the second exposure of sediment south of the main L2 section (locality 8, text-figure 4 of Young 1988). Two horizons yielding fish remains were located during 1991/92. The lowest horizon (field name LA-1) occurs about 38 m from the base and is a medium-grained clean quartzo-feldspathic sandstone containing *Bothriolepis* cf. *askinae*, *Portalodus bradshawae* gen. et sp. nov., a low-crested, finely tuberculated species of *Groenlandaspis*, with the notable absence of thelodont scales. The holotype tooth of *Aztecodus harmsenae* gen. et sp. nov., along with several other specimens came from a slightly higher horizon about 68–70 m from the base of the Aztec Siltstone. The lithology exposed here is a buff-coloured pink medium-coarse quartzose sandstone with interspersed green silts. Fish remains occur as scattered debris consisting largely of isolated, and commonly fragmented placoderm plates (*Bothriolepis* sp.), acanthodian spines and scales, and shark teeth. In addition *Portalodus bradshawae* gen. et sp. nov. also occurs in this horizon, although teeth of *Aztecodus* gen. nov. are more abundant.

Mount Feather

10. Gunn and Warren locality (57/58)

This locality has not been recollected. The original material obtained by B.M. Gunn and G. Warren included a single shark tooth described by White (1968) as the holotype of *Mcmurdodus featherensis*. Its horizon within the Aztec Siltstone is unknown.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Antarctilamna Young, 1982

Antarctilamna cf. *prisca* Young, 1982

Figures 3, 4, 13

Material

Seven isolated teeth, mostly complete: WAM 90.2.37, 92.2.2 – 92.2.6, 92.3.68.

Localities and horizon

WAM 90.2.37, 92.3.68, 92.4.5: Cook Mountains, at "Gorgon's Head", near Mt Hughes, in the upper 20 m of the Aztec Siltstone, associated with a diverse fauna including phyllolepid placoderm remains, *Pambulaspis*, *Bothriolepis*, *Groenlandaspis*, osteolepiform scales, *Gyracanthides* spines, and a lungfish toothplate resembling *Eoetenodus* sp. (Woolfe *et al.*, 1990). WAM 92.4.3, 92.2.4, 92.4.6: Mt Ritchie, middle horizon, about 120 m from base of section 24 of Young, (1988); WAM 94.2.2: Lashly Range (LA 2 site, third outcrop of Aztec Siltstone south of L2, Mt Crean main section, lower horizon).

Remarks

These specimens resemble the type material in having large divergent main cusps ornamented with 4–6 sparse ridges, and 1 to 5 small median cusps. However some come from a much higher horizon than the type material (which occurs in the lowest Aztec biozones of Young 1988). Until more material is found on which morphological differences might be demonstrated, we provisionally consider the specimens as close to the type species of *Antarctilamna*.

Description

These specimens vary in size as measured across

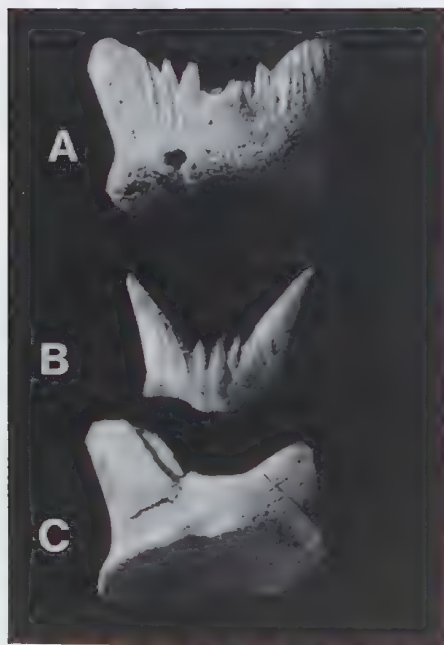


Figure 3 *Antarctilamna* teeth. A, WAM 94.2.2 from the Lashly Range (site LA-2) in labial view. B, WAM 92.3.68, from "Gorgons' Head", Cook Mountains, in labial view. C, WAM 2.3.62, from the top horizon at Mt. Ritchie, labial view. All x 8.

the base, all falling within the range of 1–4 mm described in the holotype. As noted above they resemble the type material in having two divergent main cusps, ornamented with 3–6 sparse ridges which curve up from the base. WAM 90.2.37, preserved in labial view, shows an impression where a single median cusp was present. The labial surface is somewhat weathered but still shows evidence for 3–4 weak striae on the main cusps. WAM 92.3.68 (Figures 3B,4C) has a median cusp slightly larger than the two lateral cusplets, all of which sit between the two main divergent cusps. This specimen comes from the youngest horizon at the top of the Aztec Siltstone at Gorgon's Head (Mt Hughes) and shows the base being more sub-rectangular in form rather than having a rounded lingual margin as shown in Young's reconstructed specimen (1982, text-figure 3 C). The striations extend onto the intermediate cusps (Figure 3C, 4). Between the two main cusps on WAM 94.2.2 (Figure 3A) there are two pairs of small median cusps lateral to a slightly larger central cusp that has broken off at its base. Thus there would have been five median cusps between the two divergent main cusps. The striae on this specimen number up to 7 on each main cusp and even the median cusplets have striae developed. In cross-section the cusps and intermediate cusplets are weakly compressed, almost round at the base become flatter near the apex of each cusp. The lateral and mesial edges have a sharp cutting edge running half way down the sides of each main cusp.

All the known *Antarctilamna* teeth have three or more small intermediate cusps, and of these the central cusp is slightly larger than the two or four lateral cusps, as was observed in the type material (Young 1982: 824, plate 87, figure 1; also see Appendix, Figure 13). In these specimens the number of intermediate cusps varied between two and three, but this was a much larger sample (about 65 teeth from the holotype). It is possible, however, that all *Antarctilamna* teeth from these higher horizons have three intermediate cusps, but this needs to be substantiated with a larger sample. Hampe (1993) indicated that a range of tooth abnormalities occurs in bicuspid xenacanth teeth, including the appearance of additional median cusplets. In the holotype of *Antarctilamna prisca* it was suggested that striations may be restricted to the outer surface of the crown (Young 1982: 824), and this observation is confirmed by the new specimens. WAM 92.3.62 (Figures 3C, 4A, B) shows a larger ventral foramen surrounded by some smaller foramina opening through the base, as in *Phoeodus* (e.g., *P. gothicus*; Gross 1973: plate 34, figure 15b; Ginter 1990), but not previously noted by Young (1982) in the type material. A slight protuberance on the labial margin (Figure 4A, B) is the basal tubercle corresponding to that developed

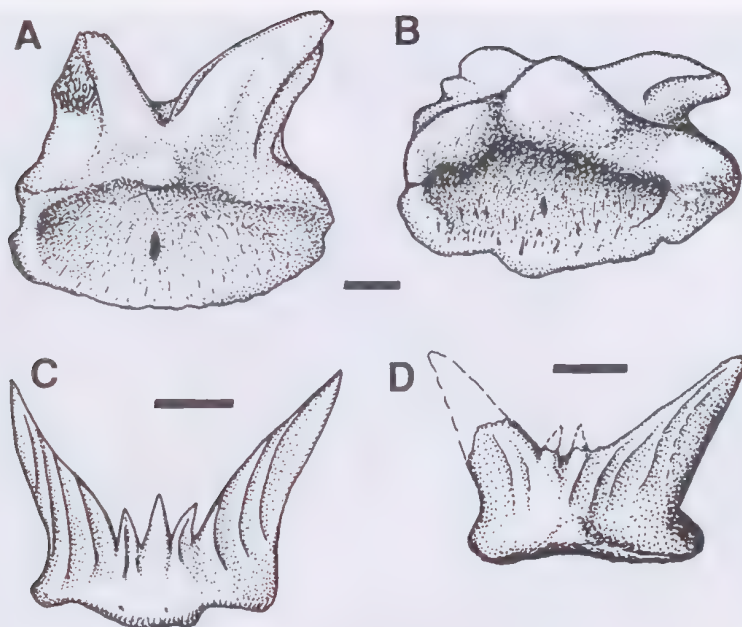


Figure 4 *Antarctilamna* teeth. A, B, WAM 92.3.62, in labial view. B, in basal view, from the top of Mt. Ritchie. C, WAM 92.3.68 from "Gorgon's Head", Cook Mountains, showing three intermediate cusps, labial view. D, a tooth from the holotype of *Antarctilamna prisca* (CPC 21187) previously illustrated by Young (1982, plate 89, figure 7), which shows two small intermediate cusps. Bar scales are all 1 mm.

in advanced xenacanth teeth (e.g., Hampe 1988a: figure 1). The corresponding region in *Phoebodus* teeth is the 'labio-basal thickening' of Ginter and Ivanov (1992, figure 2).

Stratigraphic occurrence

Antarctilamna teeth are now known from the base of the Aztec Siltstone (A. *prisca*, *askinae* zone, with thelodonts) through to the youngest biozones (occurring with phyllolepid and *Pambulaspis* at Gorgon's Head), although the latter specimens may possibly belong in a different species.

Portalodus gen. nov.

Portalodus bradshawae sp. nov.

Figures 5–7

'tooth [which] resembles the diplodont teeth found in *Xenacanthus*', Ritchie, in McKelvey *et al.*, 1972: 351.

Xenacanthus sp. Young 1982: 833, figure 3E–G, plate 89, figures 1–4.

Xenacanthus sp., Grande and Eastman 1986: 121.

'*Xenacanthus*' sp., xenacanth shark teeth, Young 1988: 13, 14, 16, figure 5.

'*Xenacanthus*' sp., Schneider 1988: 71–2, figure 2 A–C.

'xenacanth shark tooth', Young 1989a: figure 4D.

teeth of *Xenacanthus* sp.', Young 1991: figure 15.6c, d.

'xenacanthid gen. nov. 1', Young *et al.* 1993: 248.

'xenacanth shark tooth', Vickers-Rich and Rich 1993: 93, plate 82.

'teeth identified as... *Xenacanthus*', Capetta *et al.* 1993: 597.

'xenacanthid indet.', Davis 1994: 60.

'a new form of fossil shark's tooth...', Long 1995b: p.69 (photo).

Etymology

From the type locality, Portal Mountain; and in honour of K221 expedition leader Margaret Bradshaw.

Diagnosis

Shark with large diplodont teeth, base to cusp apex length up to 2 cm in largest specimens. Principal cusps divergent, one about a third larger than the other, and twisted in different planes in occlusal view. Few sparse external striae may be developed on lingual surface, but labial surface smooth. Cusps almost rounded in cross-section, slightly compressed with cutting edges developed along mesial and marginal edges. Base normally broader than the height of the shorter cusp, with a prominent labial platform, and lacking a projection on lingual face. Underside of base simple, without

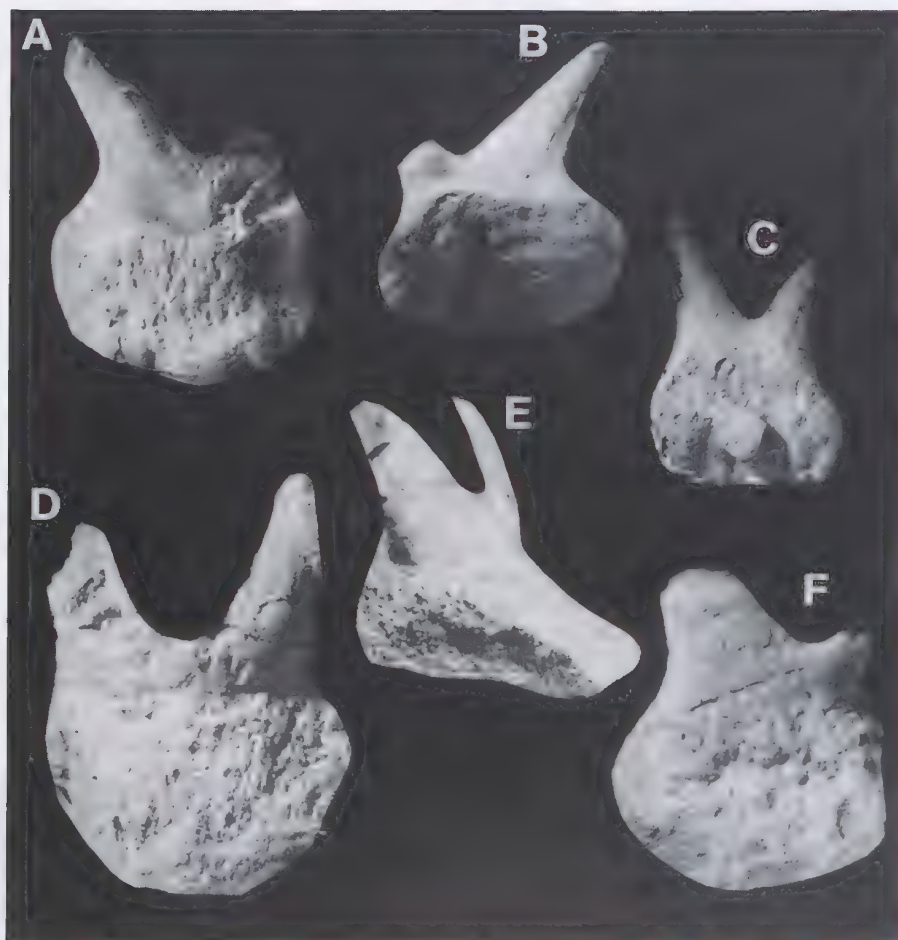


Figure 5 *Portalodus bradshawae* gen. et sp. nov. A, WAM 94.2.8., labial view, X 4. B, WAM 94.2.10., lingual view, X 4 (both from Portal Mountain, type locality). C, WAM 94.2.12., lingual aspect, slightly flattened to show basal view also, X 2, from "Gorgon's Head", Cook Mountains. D, E, Holotype WAM 92.3.60. X 4, D, labial view, E, left lateral view (Portal Mountain, type locality). F, WAM 92.3.65, labial view, from Fault Bluff, "fish hotel" B horizon. A-C are latex casts whitened with ammonium chloride, D-F are actual specimens (whitened).

well-defined ridges or transverse groove. Single large nutritive foramen and rostrocaudal groove on ventral surface.

Remarks

Young (1982: 835) oriented these teeth with the 'expanded side of the base assumed for the purpose of description to correspond to the lingual torus of other forms'. However the curvature of the cusps (which should point into the mouth) indicates that this basal projection must be an extension of the labial, not the lingual surface, and in this respect *Portalodus* gen. nov. differs from *Xenacanthus*, and all other forms with diplodont teeth, in lacking a lingual torus, and instead having the opposite surface of the base developed as a

labial projection. The only other shark tooth type known with this configuration is the genus *Omalodus* erected by Ginter and Ivanov (1992; earlier named as *Phoebodus bryanti* by Wells 1944), but this form is much smaller, and differs in having three principal cusps with smaller cusplets in between them.

Holotype

WAM 92.3.60 (Figures 5D, E; 6A), a large tooth from Portal Mountain, section 200 m west of section P1, collected by J. Long.

Other Material

Approximately 32 teeth. Portal Mountain (teeth): CPC 21214-227, 31614, AMF 54329-331, 555735,

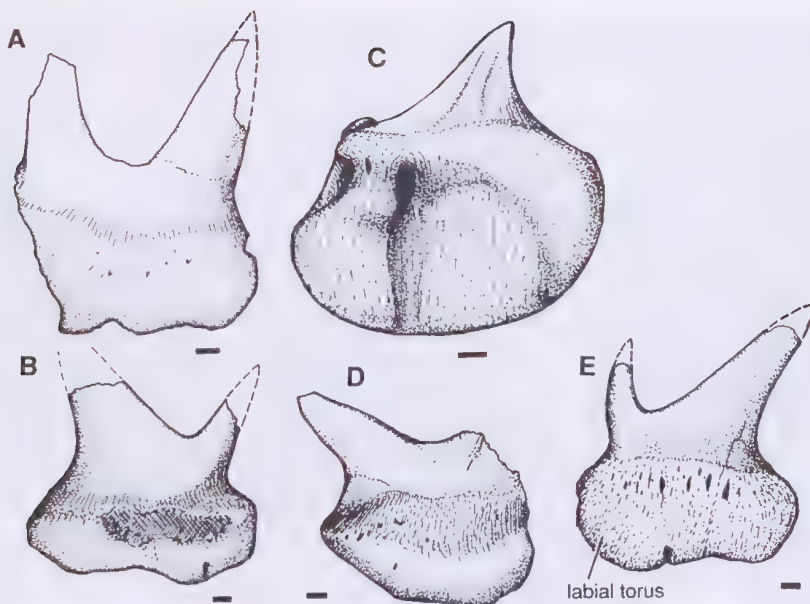


Figure 6 *Portalodus bradshawae* gen. et sp. nov. A, Holotype WAM 92.3.60, labial view. B, WAM 92.3.63, labial view. C, WAM 94.2.10 showing basal view; D, WAM 94.2.8, labial view. E, CPC 21224 (from Young, 1982 text-fig. 3F). Bar scales are all 1 mm.

from locality 11 of Young (1988), section 10 of Barrett and Webb (1973), all from unit 17 except CPC21214, 215 (from unit 26); WAM 92.3.60, 92.3.63, 94.2.1, 94.2.8, , section about 200 m west of locality 12 of Young (1988; section P1 of Askin *et al.* 1971), at approximately the same level as the upper vertebrate assemblage at locality 11 of Young (1988, figure 5; section 10 of Barrett and Webb, 1973). Portal Mountain (fin-spines): CPC 21192, AMF 55617 from units 26 and 17 may possibly belong to *Portalodus* gen. nov. (by association only). West of Mt Ritchie: CPC 21228, one tooth from locality 23 of Young (1988). WAM 92.3.65, 92.3.66., "fish hotel" site B (Fault Bluff, Cook Mountains, Figure 1). WAM 92.3.64, Mt Ritchie, middle horizon (new site 1991/92). WAM 94.2.12, "Gorgon's head" (near Mt Hughes), Cook Mountains. WAM 94.2.11, Mt Gudmundson (Cook Mountains), horizon 6. WAM 94.2.7, Mt Crean (section I2, site MC7, Young 1988).

Description

These are the largest teeth yet recorded in Devonian sharks, the biggest specimen measuring 2 cm in height from base of root to tip of crown (WAM 94.2.12; Figure 5C). Most specimens fall in the size range of 10–15 mm (maximum dimension). As originally described (Young 1982: 834, 835), these teeth were distinguished from *Antarctilamna* teeth by the unequal size of the cusps, the way the cusps were twisted in different planes in dorsal view, and in the opposite direction to the

projection of the base, the absence of central cuspules, and the deeper, more bulbous base. Each cusp is rounded in section distally, but proximally the labial face is flattened, and separated from the more rounded lingual face by a fine ridge continuous between cusps. The labial face of the cusps is smooth (Figures 5A, D, F; 7A, C), but the lingual face (Figures 5B, C; 7D) normally carries two to four coarse striations (in contrast, a smooth lingual and striated labial surface is known in some other forms, e.g., *Antarctilamna*, '*Phoebodus*' *heslerorum*; Williams 1985: 127). The base is normally notched in about the middle of its basal margin, in which a large foramen is seen in labial view (WAM 94.2.10, Figures 5B, 6C). The ventral surface of the base is shown in WAM 94.2.10 (Figure 6C, also 7B, D). There is a large foramen placed near the lingual margin, and a well-defined ledge separating the lingual half of the base from the more concave labial half. The labially-projected division of the base has a weak outer ledge developed on the dorsal surface. The ventral surface is crossed by a shallow groove connected to the foramen on the labial surface (Figures 6 C, 7B, D).

Two fin-spines (CPC 21192, AMF 55617) associated with the teeth of *Portalodus* from the type locality were assigned to *Antarctilamna prisca* by Young (1982). However, it is possible that these belong to *Portalodus*, since *Antarctilamna* teeth have not been found at this locality and horizon (units

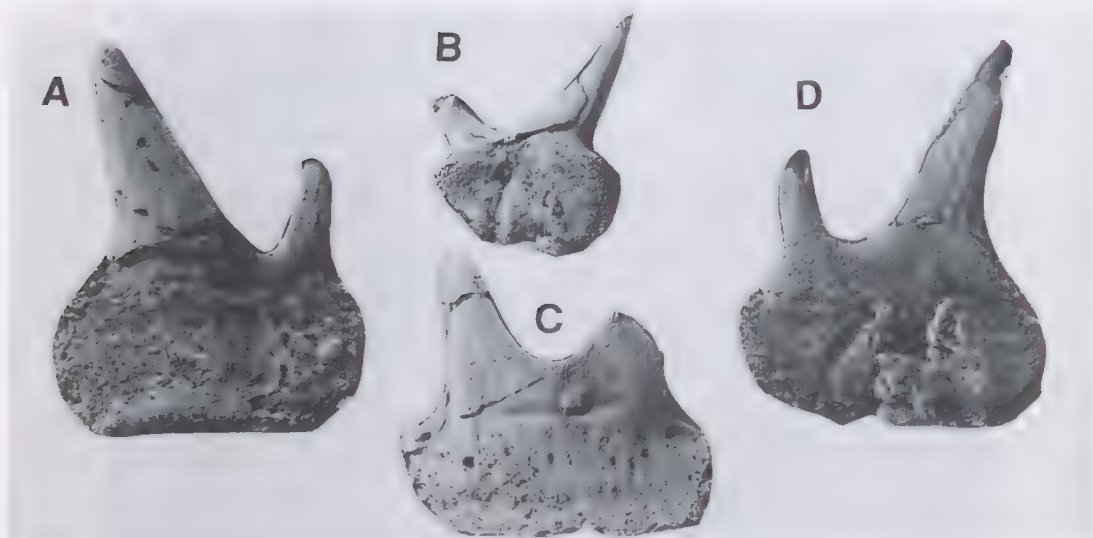


Figure 7 *Portalodus bradshawae* gen. et sp. nov., A, D, labial and lingual views of SN96a; B, lingual view of SN 96b, C, labial view of SN 93a. All x4. Latex casts whitened with ammonium chloride.

17 and 26). The figured specimen (Young 1982, plate 87, figure 2) was noted to differ somewhat in sculpture of the ridges from other spines assigned to *Antarctilamna*, and CPC 21192 has only 16 costae on one side, whereas other spines have a greater number. More material is needed to clarify whether these spines actually belong to *Portalodus*.

Stratigraphic occurrence

The type material comes from Portal Mountain, but the species is also found at "Gorgon's Head" near Mt Hughes (top level), Cook Mountains; Mt Gudmonson (level 6, top horizon), Fault Bluff, Cook Mountains, ("fish hotel" B site); Mt Crean (site MC7, Young 1988), Lashly Ranges, section "LA" (second outcrop south of Mt Crean L2 section); Mt Ritchie, horizon "M". All occurrences of *Portalodus bradshawae* gen. et sp. nov. come from above the *Turinia antarctica* biozones (first appearance within the *portalenesis* zone) and range right through to the top of the biostratigraphic zonation scheme (occurring with phyllolepis and *Pambulaspis* at Gorgon's Head).

Aztecodus gen. nov.

Aztecodus harmsenae sp. nov.

Figures 8, 9.

Mcmurdodus? cf. *featherensis* Young 1982: text-figure 3H, plate 88, figure 4

'tooth ... tentatively referred to *Mcmurdodus*', Turner and Young 1987: 236.

Mcmurdodus? cf. *featherensis*, Davis 1994: 61.

Etymology

After the Aztec Siltstone, which has produced all the known specimens, and for Dr. Fraka Harmsen, California State University at Fresno, sedimentologist on K221-A136 Expedition.

Diagnosis

Shark with diplodont teeth up to 2cm wide, with a low base which is broader than the height of the cusps. Second principal cusp of nearly equal size to approximately three-quarters the height of the largest cusp, and both cusps are widely separated by a cutting ridge bearing approximately 12 small crenulations. Cusps are smooth both lingually and labially with strongly compressed cross-sections, and well-developed cutting edges. Small accessory cusplets usually developed at mesial and marginal ends of tooth adjacent to main cusps. Base low and broad in labial view, with two transverse canals. Ventral surface of base subrectangular with gently convex margins all round, and approximately 2.5 times as long as broad.

Remarks

This genus differs from *Portalodus bradshawae* gen. et sp. nov. because it is based on broad teeth with cusps widely separated by a crenulated cutting ridge, by the low height of the base, the presence of very small accessory cusplets, and the paired transverse canals penetrating the the base. It is also generally of smaller size, although the largest specimen (WAM 92.3.59, Figures 8H, 9C) in width approaches the maximum height of *Portalodus* gen. nov. The larger size, central crenulated cutting ridge, wide separation and

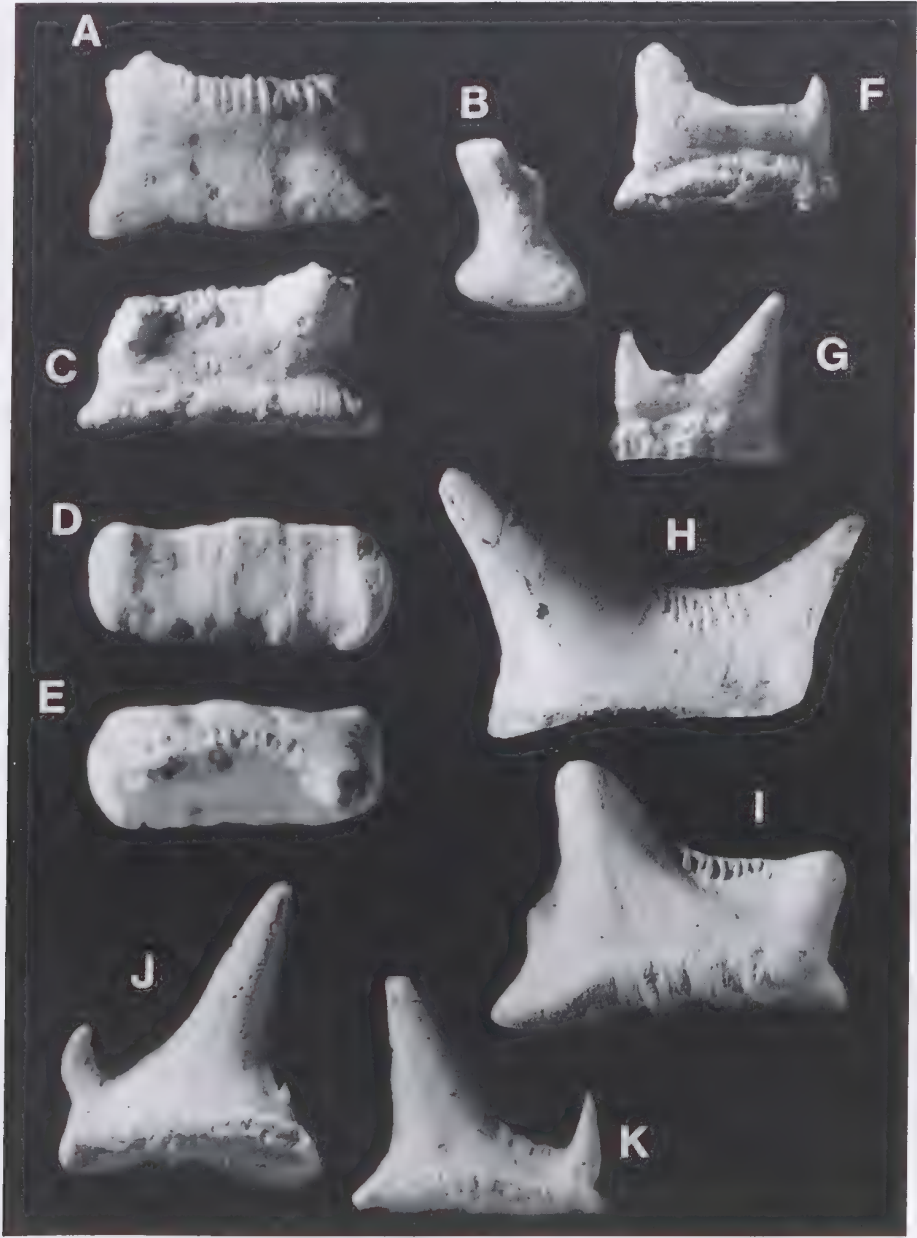


Figure 8 A–I, *Aztecodus harmsenae* gen. et sp. nov. A–E, Holotype (actual tooth) WAM 92.3.61, from Lashly Range (LA-2 site), in A, labial, B, lateral, C, lingual, D, basal and E, dorsal views, x5. F, WAM 92.3.71, in labial view, from Fault Bluff (“fish hotel” B horizon), x5. G, 92.3.70, (from LA-2), x5. H, 92.3.59, labial view, from Alligator Ridge (locality 20, top), x4. I, WAM 92.3.58, labial view, from Alligator Ridge (locality 21, top) x4. J, K, *Anareodus slatei* gen. et sp. nov. J, WAM 94.2.9, labial view, x8. K, 94.2.13, Holotype, labial view, both from Fault Bluff (“fish hotel” B horizon), x 8. A–G are actual specimens, others are latex peels; all specimens whitened with ammonium chloride.

unequal size of cusps, and the lack of striae on cusps clearly distinguish this genus from the teeth of *Antarctilamna*. No other Palaeozoic shark has widely separated divergent cusps with a well-

developed mesial crenulated region. As originally described (Young 1982: 835), this tooth type resembles *McMurdodus* in its elongate compressed form, with minor cusps at the margins of the tooth.

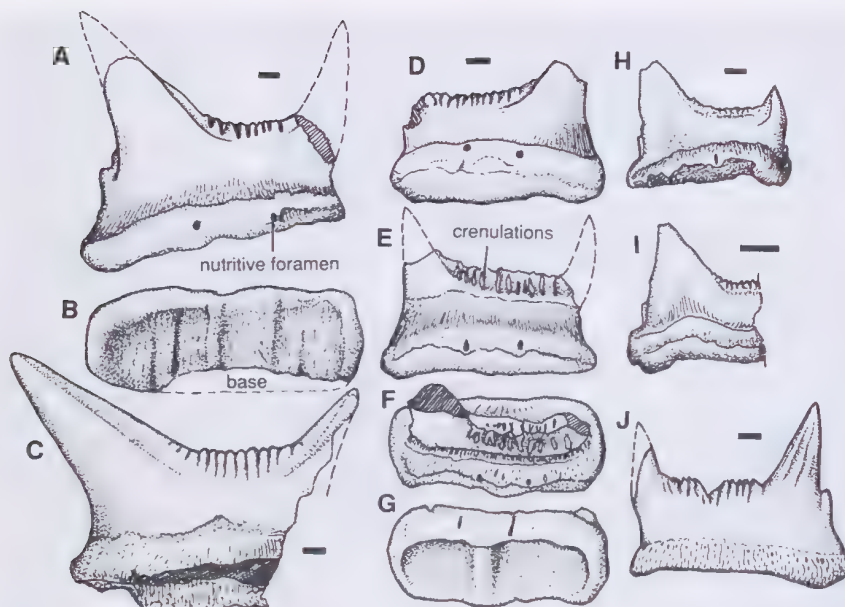


Figure 9 *Aztecodus harmsenae* gen. et sp. nov. A, B, WAM 92.3.58, labial and ventral views. C, WAM 92.3.59, labial view; D–G, holotype WAM 92.3.61, in D, lingual, E, labial, F, dorsal, and G, ventral views; H, WAM 92.3.71, labial view. I, WAM 92.3.69, from Fault Bluff, ("fish hotel" B horizon) $\times 4$. J, CPC 21229, labial view (previously illustrated by Young, 1982, figure 3H, plate 88, figure 4). All bar scales are 1 mm.

There is also a resemblance to *McMurdodus* in the shape of the base in ventral view, as subsequently described by Turner and Young (1987: figure 4B). However, the main differences lie in the larger number of cusps and absence of a lower crenulated cutting ridge in the central part of the *McMurdodus* tooth, where instead the largest cusps are situated, the lack of the ventral groove on the base, and the fact that the minor cusps at either end are directed almost horizontally in that form.

Holotype

WAM 92.3.61 (Figures 8A–E, 9D–G), from the section LA, site LA–2, Lashly Mountains, about 200 metres south of Mt Crean, from the second fish horizon (LA2) about 70–80 m above the base of the section.

Material

Six other teeth. CPC 21229, from Mt Ritchie, section A4 near units 61, 62 (figured Young 1982, text-figure 3H, plate 88, figure 4); WAM 94.2.17, from LA–2 (type locality); WAM 92.3.58, from site 20 (scree); 92.3.59, from Alligator Peak, locality 20 (top horizon); WAM 92.3.70, 92.3.71, from Fish Hotel site B, Cook Mountains.

Description

These teeth range in size from about 5 mm (92.3.70) to 16 mm across the cusps (WAM 92.3.59,

Figures 8H, 8C), being considerably wider than high, and with a distinctive almost rectangular base when viewed dorsally or ventrally (Figures 8D, E, 9B, F G). The holotype (WAM 92.3.61, Figures 8A–E, 9D–G) was extracted from *in situ*, and although the main cusps are damaged it shows the distinctive crenulated mesial edge, a feature not seen on any other Devonian sharks tooth. In this specimen there are approximately twelve small ridges forming the crenulated mesial edge which is gently curved, being weakly convex when viewed labially. The enameloid-root boundary is well defined and gently curved on the labial face. The two prominent main cusps have a strong lingual curvature and are relatively broad and flat, tapering mesially to form a sharp cutting edge before the crenulations develop (e.g., Figures 8H, I, 9A–C). The basal view (Figures 8D, 9B, G) shows the root with an anterior thickening and a few rostrocaudal ridges and weak grooves, but lacking any foramina. Two well defined nutritive foramina pass through the tooth from labial to lingual side at the level of the ventral margin of the base (e.g., Figure 9A, D, E, H). Other specimens show the same proportions as the holotype (Young 1982, text-figure 3H; Figures 8F, 9H).

Two specimens have slightly different morphologies, and come from the top of the Aztec Silstone at site 20 in Alligator Ridge, within the phyllolepid biozone of Young (1988). WAM 92.3.59 and 92.3.58 are slightly larger than the other

specimens, and have more widely splayed main cusps and, relative to the holotype, they show a more curved, and distinctly shorter, mesial crenulated area when viewed in labial or lingual aspect. WAM 92.3.58 shows the presence of a small accessory cusplet on the external edge of the main cusp, a feature seen on nearly all specimens with that edge well-preserved (e.g., Figure 9J), although absent on 92.3.59 (Figure 8H, 9C). It is possible that these two teeth could represent a different, younger species of *Aztecodus*, although as only two specimens are known, and they show only slight differences from the other specimens, we prefer to place them in the same species until more material can substantiate or refute these morphological differences.

Stratigraphic occurrence

The type material comes from the Lashly Ranges, (section "LA"); other specimens are from Mt Ritchie, section A4 near units 61, 62; from Alligator Peak, locality 20 (top horizon) and from Fault Bluff, "fish hotel" site B, Cook Mountains. The teeth all come from above the thelodont biozones, with first appearance high in the section at "fish hotel" (at least 65 m from base of unit covered by scree, occurring with phyllolepid, *Groenlandaspis antarcticus*, *Portalodus bradshawae* gen. et sp. nov., and ranging right through to about 20 m from the

top of the Aztec Siltstone at Alligator Ridge, site 20 (possibly uppermost *portalensis* or *karawaka* biozones).

Anareodus gen. nov.

Anareodus statei sp. nov.

Figures 8J–K, 10

Etymology

After ANARE (Australian National Antarctic Research Expeditions) who funded J. Long's field work, and for Brian Staite, survival leader on K221/A136 Expedition.

Diagnosis

A dipodont shark tooth with main cusps of very unequal size, separated by a mesial-marginal ridge sometimes bearing small crenulations, and a small accessory cusplet normally present on the mesial side of the main cusp. Main cusp quite flat and sigmoidally curved in lateral/mesial view. Base low, strongly concave, and rectangular in outline in basal view.

Remarks

This genus resembles *Aztecodus harmsenae* gen. et sp. nov. in sometimes showing crenulations on the central cutting ridge, in the presence of a small

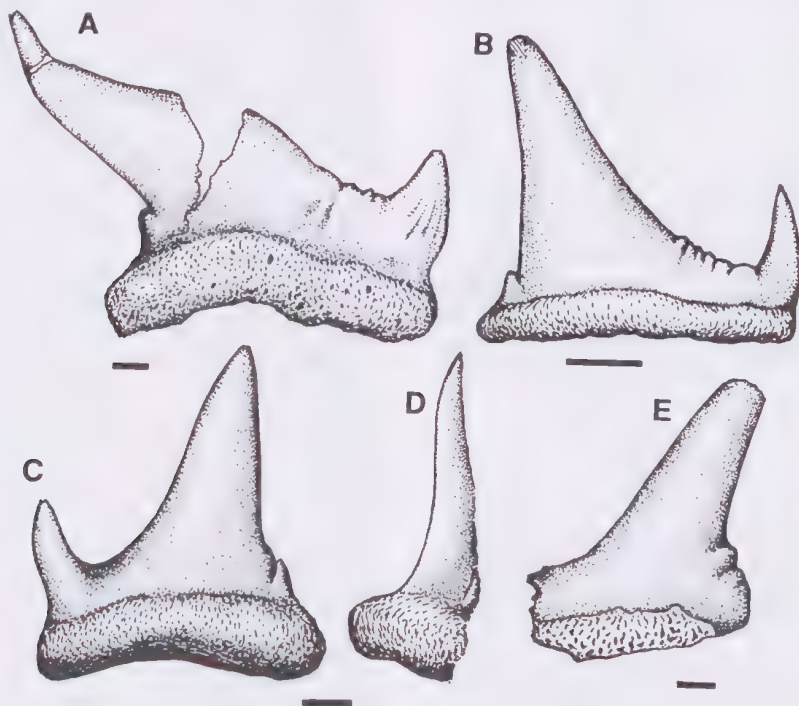


Figure 10 *Anareodus statei* gen. et sp. nov. All specimens, except D, shown in labial view; D, in lateral view. A, WAM 90.2.38, from "Gorgon's Head" (Cook Mountains). B, WAM 94.2.13. C, WAM 94.2.9 (both from Fault Bluff, "fish hotel" B horizon). E, WAM 90.2.39 (Gorgon's Head). All bar scales are 1 mm.

accessory cuspule on the lateral edge of the main cusp, and in the shape of the base in ventral view. However it differs from *Aztecodus* in having a much larger, flatter main cusp, in the more concave shape of the base, with sigmoid curvature along its length, and the absence of the two nutritive foramina.

Holotype

WAM 94.2.13, from the Fish Hotel site B, Cook Mountains (Figures 8K, 10B).

Material

WAM 90.2.38, 90.2.39 ("Gorgon's Head", near Mt Hughes, Cook Mountains); also 94.2.9 from Fault Bluff, "fish hotel" (site B), Cook Mountains.

Description

These teeth are all of small size (less than 1 cm in width or height) but nonetheless overlap in size range with both *Portalodus* gen. nov. and *Aztecodus* gen. nov., indicating that they are not likely to be juvenile or extreme posterior teeth of one of the other Antarctic genera occurring in the same horizons. The main cusp of *Anareodus* gen. nov. is relatively flat and broad quite unlike that of the previous genera, with a well-defined thin cutting edge, and lacking any external ornamentation on the enameloid. In mesial view this cusp shows a weak sigmoidal curvature (WAM 94.2.9, Figure 10D). Incipient crenulations of the type described above in *Aztecodus* are seen in two specimens (e.g., WAM 94.2.13, Figures 8K, 10B; WAM 90.2.38, Figure 10A). The base is weakly concave to almost straight. In the largest specimen, WAM 90.2.38 (base 8.5 mm width, Figure 10A) the main cusp is approximately three times larger than the other cusp and diverges from it at a right angle. There is a weak development of median crenulations on this specimen. The root is coarsely textured with three small nutritive foramina present on the largest specimen (90.2.38) but not seen on any other specimen. None of the specimens shows the basal view of the root.

DISCUSSION

Heterodonty

One of the difficulties in dealing with small samples of isolated shark teeth is the possibility of variation in tooth morphology within the species, a problem in Palaeozoic shark systematics in general (e.g., Williams 1985: 85). Many modern sharks of the Neoselachii have a heterodont dentition, for example the largest family (Carcharinidae) in which upper and lower dentitions are markedly different, and the symphyseal teeth have their own morphology (e.g., Reif 1985). Heterodont dentition

has been suggested for various Palaeozoic sharks, and demonstrated in some, for example the Pennsylvanian *Cobelodus*, with single cusped teeth in the upper jaw, and tricusped teeth in the lower (Zangerl and Case 1976: figure 16). However, recent work on forms with diplodont teeth (Hampe 1988a, b, 1989) suggests that undetected heterodonty is not a problem for this group. Thus, in *Xenacanthus* (Hampe 1988a: figure 2) the largest teeth are located in the middle region of the jaw, and small posterior teeth lack the central cusp, but otherwise there is little variation in tooth morphology, and no known differences between teeth of upper and lower jaws. This is also the case in the modern *Chlamydoselachus* (e.g., Pfeil 1983; J. Long pers. observ.), and for the present seems a reasonable inference for the chondrichthyans under consideration here.

Is *Antarctilamna* a xenacanth?

Antarctilamna prisca was placed cladistically by Young (1982: figure 9) as the sister-group to the late Palaeozoic form *Xenacanthus*, and subsequently referred to (e.g., Maisey 1984; Young 1989a) as the most primitive known member of the Order Xenacanthida Glikman 1964, a major group of late Palaeozoic elasmobranchs characterised by 'diplodont' teeth, but also by many other derived features. The original analysis of *Antarctilamna* was carried out without access to Zangerl's (1981) article, nor the description by Dick (1981) of another early xenacanth, *Diplodoseleche*, from the Early Carboniferous of Scotland. Since then, the teeth named *Leonodus* from the Early Devonian of Spain have also been referred to the Family Xenacanthidae by Mader (1986).

The proposed xenacanthid relationship of *Antarctilamna* was followed by Maisey (1984) and Lund (1985), but not by other authors (e.g., Williams 1985; Mader 1986). Zidek (1990) has argued that both tooth types described by Young (1982) (*Antarctilamna*, and *Portalodus* gen. nov. as described above) belonged to the phoebodontid ctenacanth sharks, and any affinity with xenacanthus was considered to be exceedingly doubtful. In the original cladogram (Young 1982, figure 9), previous practice was followed (e.g., Schaeffer 1981: figure 26) in using one genus, *Xenacanthus*, to represent a higher taxon (the Family Xenacanthidae of Zangerl 1981). However, there are other genera normally placed in this family which clearly have a closer relationship to *Xenacanthus*, and this has caused some confusion. The question of whether *Antarctilamna* is a xenacanth must therefore distinguish 'crown-group' xenacanthus (family Xenacanthidae) from a more inclusive higher taxon (e.g., order Xenacanthida of Zangerl 1981). Whether *Antarctilamna* is a xenacanth in this latter sense

depends partly on whether the Xenacanthida is defined as a 'stem-based' or 'apomorphy-based' clade in the sense of de Queiroz and Gauthier (1990; also Doyle and Donoghue 1993). More important, however, is the issue of whether *Antarctilamna* is better placed within the Phoeboodontidae, as Zidek (1990) has suggested. This decision must be based on synapomorphies, and there is a need to clarify the characters on which the various families are based, using a cladistic framework which distinguishes symplesiomorphy, synapomorphy, and autapomorphy. From this perspective we may consider 'crown-group' and 'stem-group' xenacanthids separately, before examining the validity of the family Phoeboodontidae.

Regarding 'crown group' xenacanthids, Zangerl (1981) recognised two xenacanth families: Diplodosselachidae and Xenacanthidae. Fritsch, 1889, the latter including three genera: *Orthacanthus*, with a straight spine of circular cross-section attached to the shoulder girdle, and *Xenacanthus* and *Pleuracanthus* with a cranial spine transversely elliptical in cross-section, but which differed in dentition and pectoral fin structure (lepidotrichia present in *Xenacanthus*). Zidek (1990, in press) provided new information on the spine of *Orthacanthus*, which is cephalic in the type (*O. cylindricus* Agassiz, 1843), but positioned above the shoulder girdle in the species '*O. senkenbergianus*' Fritsch, which perhaps may be closely related to *Diplodosselache*. Zidek otherwise recognised four valid xenacanth genera: *Expleurocanthus*, *Orthacanthus*, *Xenacanthus*, and *Triodus*. Details of tooth morphology for some of these was reported by Hampe (1988a) (*Xenacanthus*; 1988b, 1991; *Orthacanthus*; 1989, *Triodus*). These genera are distinguished by such dental characters as the height of the central cusp, the presence or absence of striations and serrated edges on the cusps, and the number of nutritive foramina on the base, as well as by numerous histological features (Hampe 1991). These are similar features to those used to differentiate phoeboodont teeth from xenacanth teeth in the Devonian, so there is little point in including these late Palaeozoic forms in comparisons of stem group taxa. However, these studies are instructive in giving an indication of variability in tooth morphology. Thus, in *Xenacanthus* there are about 16 teeth in each jaw ramus, with the largest teeth located in the middle region of the jaw, and small posterior teeth lacking the central cusp (Hampe 1988a: figure 2). Apart from this 'gradient' heterodonty (Duffin and Ward 1983), there is little variation in tooth morphology.

Regarding stem-group xenacanthids, *Antarctilamna* was considered by Zidek (1990) to be of phoeboodontid (ctenacanthoid) affinity because its teeth have bilobed bases. The Family

Phoeboodontidae was placed within the Superfamily Ctenacanthoidea by Zangerl (1981), and the latter was united with hybodonts and neoselachians on the possession of two dorsal fin spines of neoselachian morphology. However, as noted by Ginter and Ivanov (1992), the tooth character (outer pair of cusps as high or higher than main cusp) by which the family was diagnosed by Williams (1985) does not occur in the articulated specimen '*Phoeboodus*' heslerorum. Ginter and Ivanov (1992) considered this family to contain three genera: *Phoeboodus*, *Omalodus*, and *Thrinacodus*, but the last genus was earlier interpreted as a xenacanth (Johnson 1984), although subsequently included with *Phoeboodus* by Turner (1982). Long (1990: 62) included *Thrinacodus* within the Phoeboodontidae and noted similarities between the expanded root of *Thrinacodus* with that of *Phoeboodus gothicus* (Ginter 1990).

Omalodus Ginter and Ivanov, 1992 resembles *Portolodus* in the labial projection of the base, and the absence of a lingual torus. If this is the important taxonomic character, then the diplodont condition of *Portolodus* must have evolved separately from that in other forms (e.g., *Antarctilamna*, crown xenacanthids), implying that the family Phoeboodontidae containing their three genera is a paraphyletic grouping. It is clear that phoeboodontid monophyly is not well established, and there is a need to assess the polarity for a range of characters concerned with fin-spines and teeth, as analysed below.

Analysis of Morphology

Fin-spines

Zangerl (1981: figure 51) used a branching diagram ('cladogram') to place Desmodontida, Xenacanthida, Symmoriida and some other groups together with a basal node representing the absence of spines of neoselachian morphology, which he regarded as the primitive condition for Elasmobranchii. However, outgroup comparison to holocephalans, placoderms, acanthodians and osteichthyans would indicate that at least one dorsal fin-spine could be primitive, as previously argued by Young (1982) and followed by Maisey (1984) and Lund (1985). The single dorsal spine of crown-group xenacanthids, which attached to the shoulder girdle or the back of the cranium, is an autapomorphy, with the more posterior position of the spine supporting the dorsal fin in *Diplodosselache* (Dick 1981), and a specimen ascribed to *Orthacanthus* (see above), showing that this specialisation evolved within the group. Together with the unique combination of diplodont teeth and a ctenacanth-like spine, as demonstrated in *Antarctilamna*, Zangerl's hypothesis is difficult to sustain on the grounds of parsimony. Furthermore,

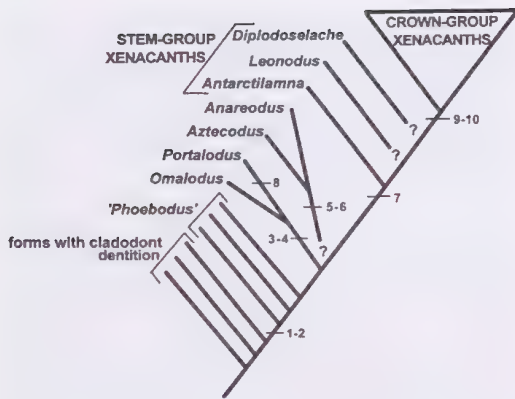


Figure 11 Cladogram summarising relationships between taxa discussed in the text, including the new forms *Portalodus*, *Aztecodus*, and *Anareodus* described here. Synapomorphies (as discussed in the text) are: 1, phoebodont tooth crown (having three main cusps, central cusp slightly smaller). 2, single button on lingual torus. 3, base with labial extension. 4, lingual torus lost. 5, crenulated mesial cutting ridge. 6, accessory lateral cusps. 7, diplodont tooth crown (central cusps much reduced or absent, two main lateral cusps). 8, diplodont tooth crown (inferred parallelism). 9, spine detached from dorsal fin, with pectoral or occipital attachment. 10, squamation lost.

that a ctenacanth-like spine is primitive for xenacanth is not inconsistent with Zangerl's suggestion that their dentition is derived from a cladodont tooth type (see below). We therefore conclude that objections to xenacanth affinity for *Antarctilamna* based on its 'ctenacanth-like' spines are concerned with symplesiomorphy, and have no foundation.

Teeth

Teeth presumably originated as modified dermal denticles, and primitively can be assumed to have resembled scales in both size and morphology (e.g., Williams 1985: 141). However, faced with the morphological range of known Devonian shark teeth (from diplodont to cladodont), either one condition must be interpreted as primitive and the others derived, or special arguments may be invoked to justify a less parsimonious hypothesis of an unknown primitive morphological type. Zangerl (1981: 7) proposed that the simplest cladodont tooth form was a single elongate crown and a small base, which could then be 'enhanced', first by expansion of the base and addition of cusps, and then by modifications in cusp size. Thus he regarded xenacanth teeth as of 'modified cladodont design' (1981: 63), thereby implying that

the cladodont condition was primitive. Lund (1985: 15) agreed that a single simple cone was the primitive tooth crown condition, using outgroup comparison with osteichthyans, but noted that the 'simplest condition known among mandibular teeth of chondrichthyans was the coronodont state: a distal-proximal series of subequal cusps fused into a 'multicuspid unit'. Lund suggested that this is plesiomorphic for elasmobranchs, and that protacrodont (low, subequal cusps), diplodont, and cladodont types are alternate derived conditions of the tooth crown developed on a 'synapomorphic' base. These alternative hypotheses of Zangerl and Lund were both apparently accepted by Williams (1985), who noted a tendency to fusion in typical anacanth branchial denticles, which could then be modified into a typical cladodont dentition by enhancement of the central cusp, and development of a lingual torus. Williams regarded these two features as advanced for all anacanthous sharks except *Cobelodus*, which he suggested exhibited the primitive condition for anacanthous sharks (where most teeth are small simple cones, with poorly developed bases, resembling the small *Petrodus*), like scales on the head of *Stethacanthus* and other form. However this interpretation has the unparsimonious consequence of requiring the evolution of multicuspid teeth in anacanth sharks independently of that in other elasmobranch groups.

Support for Lund's hypothesis is provided by the multicuspid branchial denticles observed in many forms, including *Antarctilamna* (Young, 1982: plate 87, figures 9, 10). However to interpret diplodont, cladodont and other types as alternate derived conditions of the tooth crown requires the same interpretation for the 'phoebodontid' tooth type as well, or any other combination. For heuristic reasons therefore, we provisionally follow Zangerl's interpretation that the cladodont tooth type (seen in a diversity of Palaeozoic sharks) is plesiomorphic relative to the diplodont type. We note, however, that the known fossil record (*Leonodus* of Mader 1986) suggests the opposite. The differences in tooth morphology and histology within the Family Xenacanthidae (e.g., Johnson 1980: 930; Zangerl 1981: figure 69; Hampe 1991) may be seen as variations on the diplodont theme. However the fact that the crown in xenacanthids always comprises three cusps with an orthodontine histology, which emerge separately from the base, may be derived features characterising the family (Hampe 1991), by which they are distinguished from more primitive tooth types of *Antarctilamna* and phoebodontids (but histology is not yet known in these).

Under this interpretation, the phoebodont tooth type would represent an intermediate stage of cusp reduction. Phoebodontid teeth are characterised by

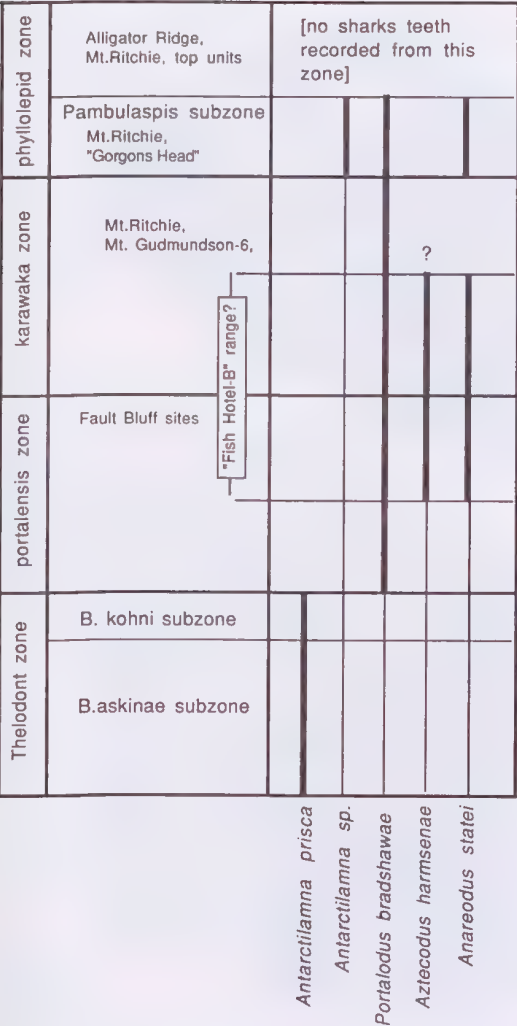


Figure 12 Summary of biostratigraphic occurrence of shark remains from the Aztec Siltstone, using overall faunal list data from new sites in Cook Mountains.

having three main cusps in the crown, with the central cusp slightly smaller; and primitively there is a bilobed base. Including smaller intermediates there may be five cusps, but specimens with four cusps are uncommon, and with six or seven extremely rare (Ginter and Ivanov 1992). Apart from reduction of the central cusp, the only other tooth character possibly uniting the group is the 30–40° inclination of the lateral cusps away from the central cusp mentioned by Zangerl (1981), but this is seen in other forms (e.g., *McMurdodus*) and is not a clear-cut character. Thus on the evidence of coronal morphology the phoebodontids would be a paraphyletic grouping.

Regarding the structure of the base, the bilobed condition in some phoebodont teeth was considered primitive for the family by Ginter and Ivanov (1992), presumably by outgroup comparison with forms like stethacanthids (e.g., Lund 1985). However, in the latter, two tubercles are developed on the dorsal surface, whereas in phoebodont teeth, including those with a bilobed base, and in all xenacanth teeth, a single 'button' is developed on the dorsal surface of the lingual torus. In *Antarctilamna*, re-examination of the tooth figured by Young (1982: figure 3C) suggests that it may be incomplete, with the base possibly larger and bilobed (M. Ginter, pers. comm.). One example of a tooth from the holotype was reported to show a 'button', but some others which apparently lacked it (Young 1982: 827) may be abraded (M. Ginter, pers. comm.), so the state of this character needs confirmation.

The lingual torus is regarded as a derived character by most authors, and is one of a variety of mechanisms evolved within the Chondrichthyes to maintain proper spacing between successive teeth in a tooth family (Zangerl 1981: 8) until they move up into a functional position (e.g., Hampe 1988a: figure 3). Thus the 'button' on the dorsal surface of the lingual torus in *Phoebodus* fits into a depression in the base of the overlying tooth (Ginter and Ivanov 1992: figure 2), with teeth presumably held together by inter-dental ligaments (Lund 1985). In various cladodont teeth the lingual torus may have two buttons developed, but the single button in phoebodont and diplodont teeth seems to be a consistent feature, and may be interpreted as a synapomorphy uniting 'phoebodontids' as a paraphyletic stem-group to xenacanth in the broad sense (see Figure 12). A differentiated 'basal tubercle', developed from a general 'labio-basal thickening' of some phoebodonts (Ginter and Ivanov 1992: figure 2), which in certain species (e.g., *P. australiensis*, Long 1990: figure 4D) is developed as a distinct 'ventro-labial boss', may define a less inclusive group (some *Phoebodus* species, and stem and crown-group xenacanth; Figure 12). It should be noted that Zidek (in Cappetta *et al.* 1993) has suggested that in the Early Devonian form *Leonodus* 'the basolabial boss and basolingual margin show a tendency toward splitting', on which evidence he suggests a possible ctenacanthoid affinity. But this resemblance, if confirmed, may be a symplesiomorphy, in which case it would indicate only that reduction of the central cusps preceded the development of a single basal tubercle in the *Leonodus* lineage. On the other hand, phoebodontid teeth, as just discussed, demonstrate the opposite situation, so there is clearly some homoplasy involved in these detailed tooth characters.

In *Omalodus* and *Portalodus*, which have a labial

extension instead of a lingual torus, the base must have been held in the tooth row in a different way. However it is not clear from its orientation whether the labial projection functioned as a spacing device.

The arrangement of foramina and canals for vascular supply to the tooth is another feature of the base which may be different in closely related forms. Hampe (1988b: figure 3a) described the system in *Orthacanthus* as two parallel, labiolingually arranged canals connected to a cavity below the crown, with a separate supply to the small intermediate cusp. In contrast, in *Triodus* there is a ramifying system to all three cusps (Hampe 1989: figure 2). In *Phoebodus gothicus* there is a single canal traversing the base (Gross 1973: 34, figure 13b), and a similar foramen is observed on the ventral face of the base in *Antarctilamna* (Figure 3A). However a different arrangement is seen in *Phoebodus australiensis*, which has two large transverse canals passing through the base (Long 1990: figure 4E). Although internal structure has not been studied, *Portalodus* (Figure 6C) and probably *McMurdochodus* (Turner and Young 1987: figure 3B) show labial and lingually placed foramina on the base, with the intervening canal partly or wholly enclosed, or expressed as a groove across the ventral surface – a combination of the supposedly distinctive types of vascularisation pattern illustrated by Duffin and Ward (1983: figure 4A–C). It is not clear at present that these different patterns have any phylogenetic significance.

Relationships of the new taxa

Based on the foregoing discussion, the three new taxa described above may be placed in a provisional cladistic framework (Figure 11). All the new taxa are variants on the dipodont pattern, with largest cusps placed at the lateral margins rather than centrally, as in cladodont teeth. However *Aztecodus* and *Anareodus* share features not seen in *Portalodus* (crenulated cutting ridge, small accessory cusps at lateral margins of crown), which we assume to indicate a close relationship. On the other hand, *Portalodus* resembles the genus *Omalodus* erected by Ginter and Ivanov (1992: 62) in the absence of a lingual torus, and development of a labial extension to the base, which forms an obtuse angle with the crown. By outgroup comparison (e.g., *Antarctilamna*, '*Phoebodus*', '*Cladodus*' tooth types), the labial extension is interpreted as a unique derived feature, whereas the absence of a lingual torus must be a secondary loss. On available evidence therefore we consider *Portalodus* and *Omalodus* immediately related, and *Aztecodus* and *Anareodus* immediately related as two sister-group pairs. This implies that the dipodont condition evolved independently in *Portalodus*, and as discussed above there may be

other evidence based on character distribution which indicates further homoplasy in this feature. However, for the present we suggest that the dipodont condition of *Antarctilamna*, *Diplodoselache*, and crown group xenacanth is a synapomorphy by which those taxa are grouped together. Lacking information on other features (e.g., fin-spine morphology), the *Aztecodus*–*Anareodus* clade does not have a clear position either within or outside the Xenacanthida on available evidence.

Biostratigraphy

The use of Devonian shark teeth in biostratigraphy is becoming increasingly important. Many new species have been recently identified and their age ranges tied into well-dated sections, some intercalated with marine sections containing conodonts or spore zonations (Turner 1982, 1990, 1991, 1992, 1993; Turner and Young 1987; Long 1990; Ginter 1990; Ginter and Ivanov 1992). Ginter and Ivanov (1992: figure 9) summarise the biostratigraphic distribution of *Phoebodus* teeth through the Late Devonian of eastern Europe in relation to the standard conodont zonation. They note their absence thus far from the early Frasnian, and rarity in the latest Frasnian *linguiformis* Zone level in sequences in Moravia (Hladil *et al.* in press) which may be due to the Kellwasser extinction event. Phoebodont maximum diversity apparently corresponds with that of palmatolepid conodonts in the Famennian, and their widespread distribution is indicated by occurrences in Australia (Turner 1982), Thailand (Long 1990), and Morocco (Derycke 1992).

Ginter and Ivanov (1992) give the earliest occurrence of *Phoebodus* teeth as the Givetian of North America (Paul Frank Quarry bone beds), and they also record Givetian occurrences from Poland, Australia, and the Kutsnetz Basin. Stritzke (1986) figured a phoebodont tooth from the *hermanni-cristatus* conodont zone of the Rhenish Schiefergebirge, Germany. The new Antarctic taxa are of similar age (see discussion in Young 1988: 16–19). The biostratigraphic distribution of the new taxa in Antarctic sections is summarised in Figure 12, and corresponds to zones 6a–e in the scheme of Young (1993), which are provisionally equated with varcus to *hermanni-cristatus* Zone conodonts (Givetian).

An older '*Phoebodus*' tooth from the Jauf Formation of Saudi Arabia (Forey *et al.* 1992) is a considerably large tooth that has very small central cusps. It has been studied by one of us (JAL) and is not regarded here as properly referred to the genus. Zidek (in Cappetta *et al.* 1993) considered the earliest *Phoebodus* to be of Eifelian age (*P. floweri*, a form synonymised with *P. fastigatus* by Ginter and Ivanov 1992), but his evidence of age is

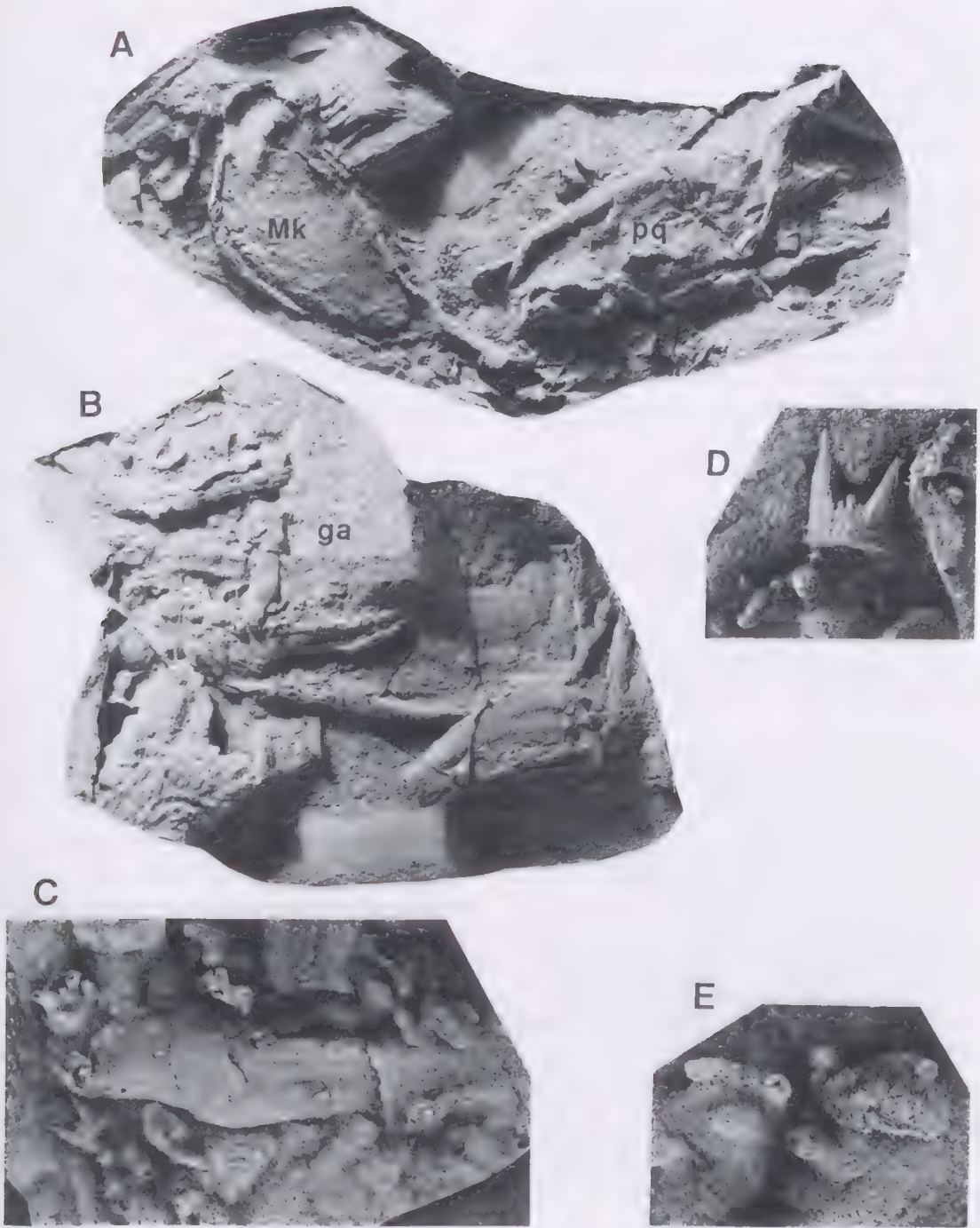


Figure 13 *Antarctilamna prisca* Young 1982. CPC 21213, Bunga Beds, south coast of New South Wales. A, latex cast showing impressions of the palatoquadrate (pq) previously illustrated by Young (1982, fig. 8C) and associated meckelian cartilage (Mk, x1). B, latex cast of counterpart to A, showing associated gill-arch elements (ga) and teeth (x1). C, detail of gill arch element shown in B, with associated teeth (x 4). D, teeth from lower left of C showing striations on labial side of cusps (upper tooth) and small cusplets lateral to major cusps (lower tooth, base obscure; x 4). E, teeth from top right corner of C showing the button on the lingual torus (x4).

not provided. *Omalodus bryanti* Ginter and Ivanov 1992, is recorded from the late Givetian of the Kuznetsk Basin, but the original material of Wells (1944) came from the same locality as *Ph. floweri* (Kiddeville bone-bed, lower part of Boyle Limestone), and this was also regarded by Wells (1944) as Givetian in age.

Biogeography

The diversity of middle Palaeozoic chondrichthyans from the Gondwana continents resulting from new discoveries over the last 15 years indicates that a substantial part of their fossil record is not represented in the well-studied Palaeozoic successions of the Northern Hemisphere. The only possible chondrichthyans (based on teeth) from the Early Devonian of the Euramerican or Asian terranes is material of *Doliodus problematicus* from the Emsian of Campbelltown, New Brunswick, Canada. This material, now housed in the Natural History Museum, London, was originally described by Woodward (1892) as acanthodian teeth, and has been re-examined by one of us (JAL). Some teeth (e.g., BMNH 7076) show a well-developed root system with vascular canals present, a characteristic of chondrichthyan teeth. Despite this, most of the record of Early Devonian sharks is from Gondwanan or neighbouring Gondwanan terranes, suggestive of a Gondwana origin for the chondrichthyans (exclusive of identifications based on scales alone).

Apart from the diplodont teeth of several taxa in the Aztec fauna dealt with above, similar teeth are also known from southern Africa (Bokkeveld Formation, upper Middle Devonian, Oelofson 1981), and South America and various parts of the Middle East have yielded similar fin-spines (but apart from Saudi Arabia, no teeth as yet). All of these areas are thought to have been part of Palaeozoic Gondwana, and a synthesis of these occurrences is given in Lelievre *et al.* (1993). Previous biostratigraphic and biogeographic assessment of the Antarctic Aztec assemblage led to the hypothesis of Gondwana origin for the xenacanth clade, and subsequent dispersal into the northern hemisphere (Young 1989a, 1990). This was in accord with evidence from a range of taxa, both invertebrate and vertebrate, indicating a biotic dispersal episode, perhaps related to changes in global palaeogeography (e.g., Young 1981, 1987).

ACKNOWLEDGEMENTS

Fieldwork in Antarctica over the 1991/92 season was funded through ASAC grant #136 to JAL, who thanks the Director and Trustees of the Western Australian Museum for their support, and field colleagues Margaret Bradshaw, Fraka Harmsen

and Brian Staite, for their assistance and support during the field trip. GCY acknowledges the assistance of Drs A. Ritchie and P.J. Barrett for his participation in the 1970–71 VUWAE 15 expedition under the New Zealand Antarctic Research Program. Field and logistic support was provided by the 197071 staff at Scott Base, US Navy Squadron VXE6, and other members of the VUWAE 15 team (R. Askin, P. Barrett, R. Grapes, B. Kohn, J. McPherson, and D. Reid). GCY also acknowledges a travel grant from the Transantarctic Association. Discussions and unpublished information on xenacanth sharks have been provided by H.P. Schultze, J. Zidek, O. Hampe, J. Maisey, and others. Dr Alex Ritchie (Australian Museum) allowed access to collections, and discussed various aspects of the Aztec fauna. Both authors acknowledge financial and other support from IGCP Project 328 (Palaeozoic microvertebrates), and extensive discussions with S. Turner and M. Ginter on fossil shark teeth. For the excellent photography we thank Kris Brimmell (WAM specimens) and R.W. Brown and H.M. Doyle (AMF and CPC specimens). Kate Trinajstić is thanked for her help editing the MS.

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The *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from Sumbawa Island, Nusa Tenggara, Indonesia

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Abstract – Two unique specimens of *Hipposideros* from West Sumbawa are described.

INTRODUCTION

Surveys of islands in the Greater and Lesser Sundas and the Maluku Tenggara region of Indonesia by staff from the Western Australian Museum and Museum Zoologicum Bogoriense, between 1987 and 1993, has resulted in the recognition and/or redefinition of a number of mammalian taxa (Kitchener *et al.* 1993 a,b). In 1988, two specimens of a unique *Hipposideros* bat were collected in West Sumbawa.

The morphology of the above two West Sumbawa specimens are herein described. They belong in the *H. bicolor* group of Hill (1963). This group is characterised by: small to moderate body; large, broadly rounded ears, normally with an internal fold or thickening of the membrane of the ear at the antitragal lobe; elongate, narrow skull; moderately inflated braincase; narrow rostrum; unspecialised auditory region; upper incisors weak with outer lobe obsolescent or obsolete; and outer lower incisor crown dimensions subequal to those of the inner lower incisor.

METHOD

Measurements were recorded with vernier calipers. For skull, dentary, dental and baculum, measurements to 0.01 mm; for externals to 0.1 mm. Terminology used in the description of characters follows Hill (1963) and Smith (1984). Measurement points, where not explicit, are detailed in Kitchener and Maryanto (1993). Pelage colour description, when following the terminology of Smithe (1975), are capitalised.

SYSTEMATICS

Hipposideros sp. indet.

Material examined

Museum Zoologicum Bogoriense No. MZB 15905, adult male carcase weighing 9.5 g; fixed in

10% formalin and preserved in 75% ethanol; skull and mandible separate; liver stored in ultrafreeze at the Western Australian Museum (WAM); collected by D.J. Kitchener, R.A. How and Maharadatunkamsi, on 26 May 1988. WAM M 31489; adult male weighing 9.8 gm; carcase and liver preserved as for the holotype; skull removed and lost.

Locality

Collected from a small cave near the main limestone "cathedral" cavern of Gua (=cave) Batu Tering, 3 km S Desa Batu Tering, West Sumbawa (c. 8°48'S, 117°22'E), at an altitude of ca. 200 m. A stream passes within a few metres of this small cave. The surrounding vegetation is dense gallery rainforest.

Characteristics

A member of the *H. bicolor* group (*sensu* Hill 1963) but separated from all other members of that group by the following combination of characters: moderately large size with forearm length 47.9–48.0, condylocanine length 16.7, and C¹M³ length 5.7; lateral supplementary leaflets on face absent; anterior upper premolar (PM²) present, only slightly extruded from toothrow but separates canine from PM¹; anterior lower premolar (PM₂) length subequal to second lower premolar (PM₄); PM₂ height three-quarters that of PM₁; anterior leaf without median emargination; posterior leaf with three well defined septa; internarial septum slightly thickened; interorbital region constricted; glandular ridge on muzzle beneath margin of anterior leaf absent; anterior half of zygomatic not particularly slender; superior projection of zygomatic poorly developed; vomer posterior projection into mesopterygoid fossa blade-like, only very slightly thickened; and baculum moderately long (3.2), straight, narrow, bifurcated at distal tip with cranial proximal (projecting) margin of base evenly rounded and not bifurcated.

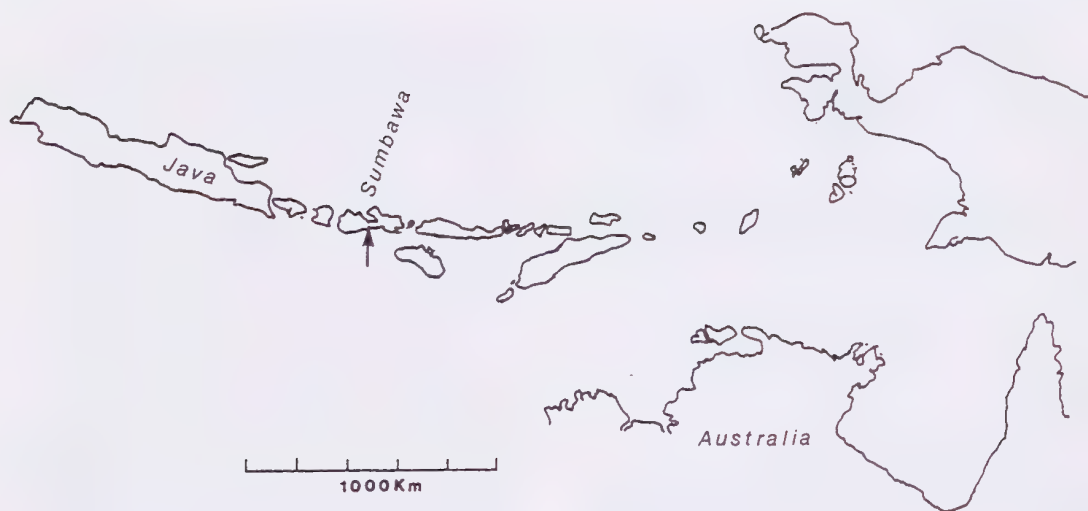


Figure 1 Location of Sumbawa Island and the locality of *Hipposideros* sp. indet.

Skull (Figure 2)

Moderately long, with greatest skull length 18.36 and condylocanine length 16.72, and slender; zygomatic width 9.43, considerably greater than mastoid width 9.05; cranium comparatively broad 8.81 and inflated; interorbital region much narrower than distance between anteorbital foramina 2.84 *v.* 5.15; sagittal crest low, reaches maximum height at cranial apex; rostral eminences slightly inflated, in lateral profile a little below junction of sagittal and supraorbital crests; in lateral profile, rostrum anterior edge slopes slightly downwards anteriorly and curves smoothly to maxilla; zygomata robust, superior jugal projection low; anteorbital foramen oval, closed by moderately wide bar of bone; premaxillae broad and closely oppose lingual margin of upper canine; premaxillae junction with a V shape; palate posterior margin a broad V shape without a median posterior spicule; mesopterygoid fossa narrow 1.74, projecting vomer blade-like, only very slightly thickened; sphenoidal bridge wide, viewed ventrally almost conceals sphenorbital sinus; sphenoidal depression, shallow, oval and wider than mesopterygoid fossa 3.02 *v.* 1.74; cochlea (the cochlea part of the petrosal) size moderate, their breadth considerably greater than their distance apart 2.64 *v.* 1.63; cochlea inflated, reaches depth level with tympanic bulla; tympanic bulla short, subequal in length to cochlea breadth, terminate *c.* 0.2 posterior to glenoid fossa margin.

Dentition

Upper incisors small, their tips markedly convergent, outer lobe obsolescent; anterior upper premolar (PM²) small, basal surface area approximately that of upper incisor, slightly

extruded from toothrow but such that C¹ is not in contact with PM⁴; M³ premetacrista half length of its preparacrista; M² and M³ with pronounced hypocone; M¹ components of eocrista shorter than those of M² but lengths of these teeth subequal; outer lower incisor crown area about 15% larger than that of inner lower incisor; anterior lower premolar (PM₂) 80% length and three-quarters height of PM₄.

Externals (Figure 3)

Ears of moderate length 18.7–19.3, rounded, anterior margins strongly convex, posterior margin with very slight concavity immediately behind apex; antitragus with distinct fold; noseleaf simple; anterior noseleaf narrower than posterior noseleaf *ca.* 5.1 *v.* 5.8; lateral supplementary facial leaflets absent; internarial septum slightly expanded laterally, more so anteriorly to a maximum breadth of 0.8, vertically it is raised in a semicircle to a height of *c.* 1.0; laterally separated from anterior edge of nares by deep grooves; narial lappets border external narial margin, raised *c.* 0.4 above surface of anterior noseleaf; intermediate leaf unspecialised; posterior leaf supported by three prominent septa.

Fur long, mid dorsal *c.* 8.5, mid rump *c.* 12.0 chest *c.* 7.5, external pinna furred to apex *c.* 9.0. Dorsum predominantly Cinnamon colour of distal one-quarter of hairs of which basal part a dull White; face Tawny. Venter, including chin, pale Smoke Gray; patagia Olive Brown.

Penis long 8.8, lightly furred; glans penis flattened in craniocaudal axis, distal tip evenly semicircular except for two small projecting lobes surrounding the urethral opening (Figure 4). Baculum moderately long 3.22, thin, straight



Figure 2 Photograph of skull, dorsal, lateral and ventral (as stereopair) view and dentary of *Hipposideros* sp. indet. from Sumbawa (MZB 15905).

cranial aspect, with distal tip bifurcated, caudal aspect of bifurcation slightly grooved, base with cranial part extending posteriorly beyond caudal part, cranial part with posterior margin smoothly convex, caudal margin of base bifurcated, base lateral breadth 0.41, base craniocaudal breadth 0.50 (Figure 5).

Measurements

External measurements of MZB 15905 are followed by those of WAM M31489. Greatest skull length (posteriormost point to C¹ alveoli anterior edge) 18.36; condylocanine length (to anteriormost face of canine) 16.72; cranial breadth 8.81; zygomatic width 9.43; mastoid width 9.05;

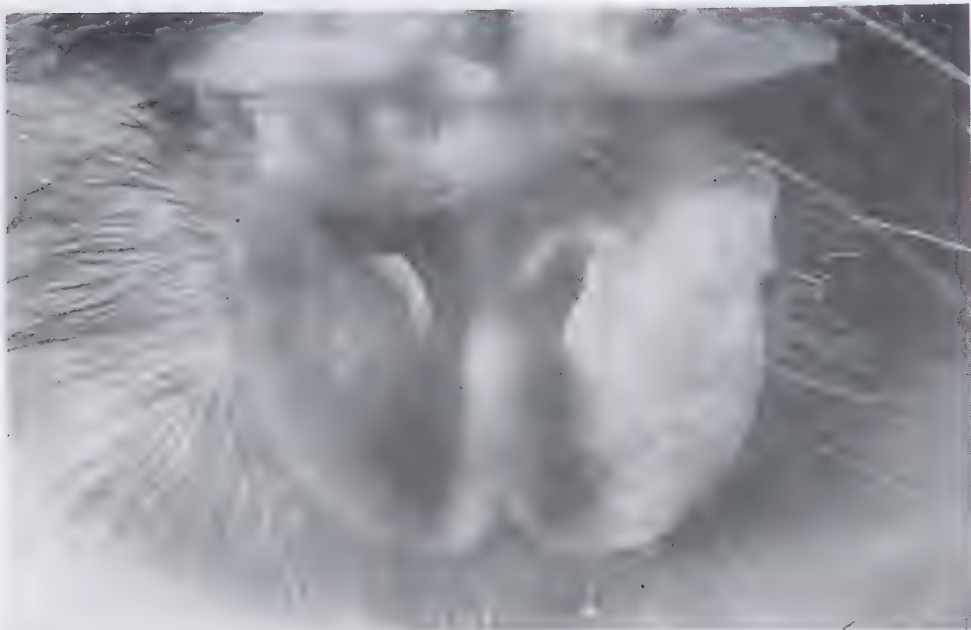


Figure 3 Photograph of face of *Hipposideros* sp. indet. (MZB 15905).

maximum cranium height 6.53; rostrum height 4.45; rostrum length 3.46; least interorbital breadth 2.84; distance between anteorbital foramina 5.05; braincase length 12.64; nasal inflation length 4.02; nasal inflation breadth 4.93; palatal length 2.60; premaxilla length 3.98; mesopterygoid fossa breadth 1.74; tympanic bulla length 2.64; tympanic

bulla breadth 1.62; cochlea length (anteroposterior diameter) 2.64; M^3M^3 breadth (alveoli, from outer edge) 5.94; C^1C^1 width (alveoli, from outer edge) 4.15; intercochlear distance 1.63; sphenoidal depression breadth 3.02; C^1 width 1.05; P^4 breadth x length 1.16 x 1.14; M^1 breadth x length 1.21 x 1.52; M^2 breadth x length 1.30 x 1.47, M^3 breadth x length 1.21 x 1.04; C^1M^3 length (alveoli) 5.70; M^1M^3 crown length 3.90; I_1M_3 length (alveoli) 7.56; dentary length (from condyle) 12.06; snout to vent length 51.0, 48.2; tail to vent length 28.6, 34.3; ear length 18.7, 19.3; tibia length 21.2, 21.0; pes length (excluding claw) 6.7, 6.6; forearm length 48.0, 47.9; digit 2 metacarpal length 38.7, 38.7; digit 3 metacarpal length 35.6, 35.5; digit 3 phalanx 1 length 19.1, 18.0; digit 3 phalanx 2 length (along

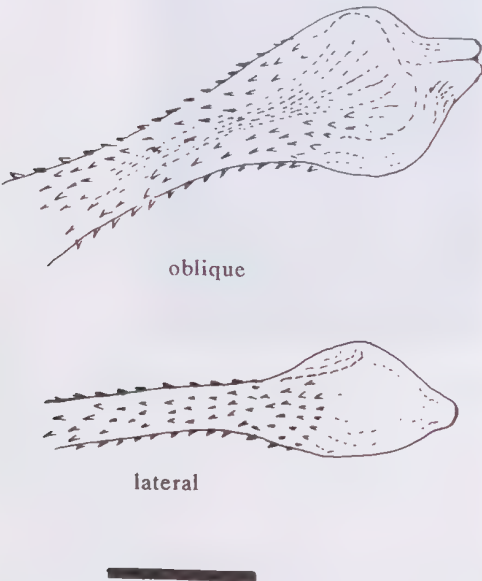


Figure 4 Drawings of glans penis of *Hipposideros* sp. indet. (WAM 31489); scale line, 1 mm.

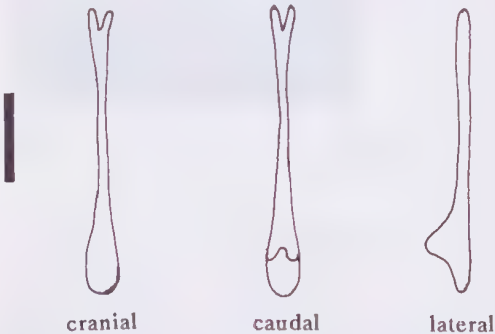


Figure 5 Drawings of baculum of *Hipposideros* sp. indet. (MZB 15905); scale line, 1 mm.

curvature) 19.2, 19.6; digit 4 metacarpal length 38.6, 37.4; digit 4 phalanx 1 length 11.4, 10.9; digit 4 phalanx 2 length 9.0, 9.7; digit 5 metacarpal length 37.2, 36.5; digit 5 phalanx 1 length 13.8, 13.4 digit 5 phalanx 2 length 11.4, 11.8; anterior noseleaf breadth 4.9, 5.3; posterior noseleaf breadth 5.5, 6.0.

Remarks

These Sumbawa specimens are a member of the *bicolor* subgroup (*sensu* Hill 1963) although it is an unusual member of this subgroup in that its zygomatic width considerably exceeds its mastoid width (9.43 *v.* 9.05) rather than being usually less than or subequal to the mastoid width. Within this subgroup they are most similar to *H. bicolor* Temminck, 1834, *H. ater* Templeton, 1848, *H. cineraceus* Blyth, 1853, *H. pomona* Andersen, 1918, and *H. macrobullatus* Tate, 1941. They are clearly distinct from *H. fulvus* Gray, 1838 and *H. nequam* Andersen, 1918, both of which are smaller and have a much reduced PM₂ (Hill 1963, Hill *et al.* 1986).

They differ from *H. ater* in being much larger (cf. forearm length 47.9–48.0 *v.* 35.0–42.5, condylocanine length 16.8 *v.* 13.2–15.0, zygomatic width 9.4 *v.* 7.0–7.6); their baculum differs greatly in size and shape (see Topál 1975).

They differ from *H. cineraceus* in being larger (cf. forearm length 32.5–36.0, condylocanine length 12.6–13.7, zygomatic width 7.0–7.6); anterior half of zygomata more robust and baculum longer and without bifurcation of projecting basal part of baculum (see Zubaid and Davison 1987).

They differ from *H. pomona* in being generally larger (cf. forearm length 37–43, condylocanine length 14.5–15.9, zygomatic width 8.3–9.0); intercochlear distance slightly larger 1.63 *v.* 1.14–1.50; tympanic bulla shorter 2.64 *v.* 2.76–3.20; and ears shorter 18.7–19.3 *v.* 20.1–23.6.

They differ from *H. macrobullatus* in being larger (cf. forearm length *v.* 40–42, condylocanine length 14.4–15.0, zygomatic width 7.9–8.3); tympanic bulla shorter 2.64 *v.* 2.90–2.94 and wider 1.62 *v.* 1.46–1.58; intercochlear distance wider 1.63 *v.* 1.27–1.45; ear shorter 18.7–19.3 *v.* 21.1–21.9.

They differ from *H. bicolor* in being larger (cf. 40–46, condylocanine length 15.4–16.3, and zygomatic width 8.6–9.5); tympanic bulla wider 1.62 *v.* 1.27–1.57 and intercochleae distance slightly narrower 1.63 *v.* 1.66–2.03; vomer projection into mesopterygoid fossa only faintly thickened; and baculum differing as for the distinction with *H. cineraceus* (measurements from Hill 1963, Hill *et al.* 1986, Hill in Corbet and Hill 1992 and J.E. Hill pers. comm.).

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of Mr J. Bannister, previous Director, Western Australian

Museum; Dr M. Amir, Director, Balitbang Zoologi (LIPI); and the Director of the Indonesian Department responsible for the conservation of wildlife in Nusa Tenggara Barat, Dr Ir. P. Supriadi, who provided us with assistance in the field, as did a number of his staff. To our colleagues Dr Ric How and Mr Ron Johnstone, Western Australian Museum, who participated in the exhausting field work, we extend our thanks for both their effort and companionship. Mrs Norah Cooper produced the photographs.

Mr John Edwards Hill provided constructive comments on the manuscript and made available measurements additional to those in the literature.

Expedition costs were defrayed by grants to Dr D. Kitchener from the National Geographic Society, Washington. Garuda Indonesia kindly defrayed freight costs of the expeditions. Mrs Susan Dalton and Mrs Anne Nevin, Western Australian Museum, typed the manuscript.

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Manuscript received 17 December 1993; accepted 21 May 1995.

The spatangoid echinoid *Schizaster (Schizaster) compactus* (Koehler, 1914) in Western Australia

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Abstract – The spatangoid echinoid *Schizaster (Schizaster) compactus* (Koehler, 1914) is recorded from Australian waters for the first time. A sample consisting of a juvenile and adults collected from off the Dampier Archipelago, Western Australia is shown to undergo significant ontogenetic variation in a number of parameters, notably number of pore pairs in all aboral ambulacra; relative size and shape of the peristome and periproct; relative width of ambulacrum III aborally; and relative length of the posterior petals. A number of morphological characters also show appreciable intraspecific variation, in particular the number of gonopores; position of the peristome; the width of the plastron; test width; and position of the apical system. An understanding of the degree of phenotypic variation in this species aids in the delimitation of species of *Schizaster* and in the characterisation of the taxa *Schizaster* and *Paraster*.

INTRODUCTION

On July 27, 1982 a number of large steel pipes destined for the North-West Shelf Gas Project was inadvertently sunk in about 45 m of water north of Dampier, Western Australia at 20°19'33.1"S, 116°33'22.11"E. Nearly 10 months later, on May 18, 1983, the pipes were recovered. They were found to be packed with soft, foraminiferal-rich silt, within which were living five species of spatangoids. In addition to 33 complete and broken specimens of a species of *Schizaster*, single specimens of *Moiria lethe* Mortensen, 1930; *Metalia sternalis* (Lamarck, 1816); and *Lovenia elongata* (Gray, 1845) were found in the silt, along with three specimens of an undescribed species of *Metalia*.

The species of *Schizaster* (Figure 1) is identical to a single specimen described by McNamara and Philip (1980a) from Rosemary Island in the Dampier Archipelago, and referred by them to *Schizaster (Schizaster) lacunosus* (Linnaeus, 1758). Examination of the larger population has revealed the species to be conspecific with a form described by Koehler (1914) from the Bay of Bengal and called by him *Paraster compactus*. However, in one character the Western Australian form differs from the features described by Koehler, and that is in the number of gonopores. Koehler's description was based on only two specimens. This difference is not considered to be of sufficient importance to warrant placing the Australian form in a separate species, as other species of *Schizaster* have been shown to possess variable numbers of gonopores (McNamara and Philip 1980a).

In addition to describing this species from the eastern side of the Indian Ocean for the first time, the aim of this paper is to demonstrate not only the variability in the number of gonopores within a single, presumably genetically homogeneous, population. This feature has been used as a generic or subgeneric character within schizasterids. In this paper characters other than gonopore number are used to differentiate the three subgenera of *Schizaster* (*Schizaster*, *Paraster* and *Ova*) and revised diagnoses of these subgenera given. This paper also aims to illustrate the extent of morphological variation present in other characters throughout ontogeny. Phenotypic variation encompasses not simply the morphological differences between adults within a population, but also differences that occur through the ontogenetic development. After all, the adult phenotype is a product of the morphological variation that the individual undergoes throughout its ontogeny.

It is particularly important to determine the degree of morphological variation present within species of *Schizaster* in order to delineate fossil taxa effectively. In the past many species have been described, particularly last century, on the basis of few specimens (Koehler's *Paraster compactus* being a case in point). Consequently, Lambert and Thiéry (1925) and Kier and Lawson (1978) recorded that up until 1970, 275 species of *Schizaster* and *Paraster* had been described. Categorising the degree of intraspecific morphological variation within this northwestern Australian species of *Schizaster* will therefore provide a useful tool to further studies

aimed at clarifying the number of species of *Schizaster*.

The other aspect of this study is to document the ontogenetic development of the species, as both juvenile and adult specimens are present within the population that was collected. McNamara and Philip (1980a) documented a number of ontogenetic changes in another Australian species, *Schizaster (Ova) myorensis*. Defining the characters that undergo morphological change during ontogeny in the northwestern Australian species of *Schizaster* will assist in determining the universality of ontogenetic change in suites of characters within the genus *Schizaster* and so aid the elucidation of the phylogenetic history of the genus.

MATERIALS AND METHODS

Measurements were carried out on 26 specimens. These are registered in the collections of the Western Australian Museum under the numbers 132–93 to 135–93. Measurements were made using electronic callipers to an accuracy of 0.1 mm. Measurements were made of test length; maximum test width; maximum test height; centre of apical system to anterior ambitus; width of aboral ambulacrum III; length and width of anterior petals; length and width of posterior petals; width and length of peristome; width and length of periproct; length from anterior of peristome to anterior ambitus; maximum width of plastron. Furthermore, counts were made of the number of gonopores and number of pore pairs in ambulacra I, II and III aborally. For the purposes of ascertaining the number of gonopores present in the species 27 specimens were studied.

SYSTEMATIC PALAEONTOLOGY

Order Spatangoida Claus, 1876

Family Schizasteridae Lambert, 1905

Genus *Schizaster* L. Agassiz, 1836

Type species

Schizaster studeri L. Agassiz 1836, by subsequent designation of the Thirteenth International Congress of Zoology in Paris; opinion 209, 1954.

Subgenus *Schizaster* L. Agassiz, 1836

Emended diagnosis

Moderate to deeply incised ambulacrum III aborally, in which pore pairs are numerous (more than 15 in each row), occur in regular, single series and are aligned transversely, or only slightly obliquely.

Remarks

In his description of the fossil spatangoid echinoids of Cuba, Kier (1984) addressed the question of the validity of the taxon *Paraster*. Traditionally, *Schizaster* and *Paraster* had been distinguished on the basis of the number of genital pores, *Paraster* having four, *Schizaster* having two (Mortensen 1951). The two taxa had either been regarded as being of separate generic status (Mortensen 1951; Chesher 1966, 1972; Kier 1975) or only subgeneric status (Kier 1957; Henderson 1975) on the basis of this character.

With the discovery that within a single population of *Schizaster (Ova) myorensis* the number of genital pores may vary between two, three and four (McNamara and Philip 1980b), other criteria were employed to distinguish *Paraster* from *Schizaster*. McNamara and Philip (1980a,b) regarded the two as subgenera and characterised *Paraster* as having a more shallow ambulacrum III than *Schizaster*, with fewer, oblique pore pairs; a more circular test; more central apical system; and straighter, more divergent anterior petals. They noted, however, that the two subgenera lie at either end of a morphological continuum, and that some species are therefore likely to be transitional between the two subgenera.

In their analysis of the evolution of the Australian species of *Schizaster* (s.l.) in the Tertiary, McNamara and Philip (1980b) noted that those species with the *Paraster* morphology were restricted to coarser sediments than those species with the *Schizaster* (s.s.) morphology. They suggested that this indicated evolution of the finer-grained sediment dwelling *Schizaster* (s.s.) morphotype from the coarser-grained sediment inhabiting *Paraster* morphotype. A similar evolutionary trend has been observed in the genus in the Pyrennees (J. Villatte, pers. comm.). Although both the Australian living and fossil species of *Schizaster* (s.l.) can be accommodated comfortably within the two subgenera *Schizaster* and *Paraster* on the basis of characters suggested by McNamara and Philip (1980a,b), Kier (1984) was unable to separate all of the 16 Cuban species of *Schizaster* (s.l.) into the subgenera *Schizaster* and *Paraster*.

However, it may be possible to subdivide *Schizaster* (s.l.) on the basis of the nature of ambulacrum III aborally, principally using a combination of the depth of ambulacrum III and the number and orientation of pore pairs. In those species with very shallow ambulacrum III, the number of pore pairs is much fewer than in those species with a deeper, broader ambulacrum III. Furthermore, the pore pairs are much more obliquely aligned, with the inner pore of each pair set much farther forward than the corresponding outer pore, such as in the sand-inhabiting *Paraster*



Figure 1 *Schizaster (Schizaster) compactus* (Koehler, 1914) from the Dampier Archipelago, Western Australia. WAM 133-93: A, aboral surface, stereo pair; B, adoral surface; C, lateral view. WAM 132-93, juvenile: D, aboral surface; E, adoral surface; F, lateral view. All $\times 2$.

floridiensis Kier and Grant 1965 (see also Chesher 1966). In *Schizaster* (s.s.) ambulacrum III is deeper, the pore pairs are more numerous (although in single rows) and aligned transversely, or nearly so (e.g., Mortensen 1951, p.301, figure 140; McNamara and Philip 1980a, figure 4D). Species with this morphology are known to be able to burrow in mud. Thus of the Cuban species of *Schizaster* recognised by Kier (1984), *S. camagueyensis*, *S. cubitabellae*, *S. fernandezi* and *S. subcylindricus* can all be assigned to the subgenus *Paraster*, as all have a shallow ambulacrum III with a relatively small number (less than 15) of obliquely aligned pore pairs, whereas *S. bathypetalus*, *S. delgadoi*, *S. egozcuei*, *S. gerthi*, *S. llagunoi*, *S. munozi*, *S. nuevitasensis*, *S. formelli*, *S. rojasi*, *S. sanctamariae* and *S. santanae*, with their greater number of transversely orientated pore pairs, can be accommodated within the subgenus *Schizaster*. It is worth noting that one of the principle characteristics of the type species of *Paraster*, *P. gibberulus*, is its possession of very obliquely arranged pore pairs in ambulacrum III aborally (Mortensen 1951, p.220, figure 104b), while in *S. studeri*, the type species of *Schizaster*, the pore pairs are closely spaced, transverse and numerous (Mortensen 1951, p.297, figure 136).

Species of *Schizaster* in which the pore pairs are so crowded in ambulacrum III that they effectively

form multiple rows (see McNamara and Philip 1980a, figure 5C), are classified as a third subgenus, *S. (Ova)*, as typified by forms such as *S. (Ova) myorensis* McNamara and Philip 1980a. Consequently a morphocline of increasing concentration of pore pairs in ambulacrum III aborally exists from *S. (Paraster)*, through *S. (Schizaster)* to *S. (Ova)* (Figure 2).

Schizaster (Schizaster) compactus (Koehler, 1914) Figure 1

Paraster compactus Koehler, 1914: 180; Mortensen 1951: 221-223, plate 24, figures 3-8, plate 52, figures 1,3; Ghiold 1989: 117, 140.

Schizaster (Schizaster) lacunosus (Linnaeus): (pars) McNamara and Philip 1980a: 129-131, figure 1.

Schizaster (Schizaster) compactus (Koehler): McNamara and Kendrick 1994: 46.

Material Examined

Australia: Western Australia: WAM 1488-75, dredged from a depth of 4-5 m outside Norbill Bay, Rosemary Island, Dampier Archipelago; WAM 132-93 to 135-93, 33 complete and broken specimens from a depth of 45 m north of Dampier, at 20°19'33.1"S, 116°33'22.11"E.

Description

Test tumid (Figure 1A,C), reaching up to 33.5 mm TL; anterior notch moderately developed (Figure 1A,B); highest posteriorly in interambulacrum 5, just posterior of apical system, forming a prominent keel (Figure 1C); height 63–72%TL (mean 67.5; SD=2.6; n=23); wider than long, ranging between 87–97%TL (mean 91.7; SD=4.6; n=26). Position of apical system variable; posteriorly eccentric, 56–65%TL (mean 60.0; SD=2.4; n=25) from anterior ambitus; ethmolytic, with two to four genital pores (Figure 3) (see below).

Ambulacrum III relatively broad (Figure 4A), 18–25%TL (mean 20.8; SD=1.7; n=25); moderately deeply incised (Figure 1A), shallowing slightly near ambitus; bears up to 38 pore pairs; smallest with 18 (Figure 5C); within a pair each pore separated by raised interporal partition; pores almost transversely aligned in a pair, although becoming slightly oblique abapically. Anterior petals moderately deep; broad, width 9–13%TL (mean 11.1; SD=0.87; n=26); diverge anteriorly at about 80° (Figure 1); slightly flexed distally; relatively long, 33–42%TL (mean 36.3; SD=2.0; n=26); bear up to 31 pore pairs (Figure 5B); pores within each pair widely spaced, elongate, not conjugate. Posterior petals slightly shallower and much shorter than anterior pair (Figure 1A), length 12–21%TL (mean 17.5; SD=1.8; n=25); width 8–10%TL (mean 8.7; SD=0.67; n=25); bear up to 20 pore pairs in each

row (Figure 5A). Peripetalous fasciole very broad (Figure 1A) and moderately indented between anterior and posterior petals. Lateroanal fasciole very thin.

Peristome lunate (Figure 1B), width 14–20%TL (mean 17.4; SD=1.6; n=24); slightly sunken; situated 16–24%TL (mean 19.0; SD=2.1; n=24) from anterior ambitus. Labrum narrow and long; anteriorly acuminate medially and projecting antero-ventrally (see McNamara and Philip 1980a, Figure 1D). Phyllode with unipores: 10 in ambulacra II and IV; 5 in ambulacrum III; 6 in ambulacra I and V. Periporal area slightly swollen around abambital unipores, but flat around adambital unipores. Plastron slightly convex; width 38–46%TL (mean 41.9; SD=2.1; n=23). Periproct ovate; length (Figure 6D) 13–21%TL (mean 16.3; SD=1.6; n=26); width (Figure 6C) 11–15%TL (mean 11.4; SD=0.92; n=26).

Ontogenetic Variation

The 26 specimens of *Schizaster compactus* range in test length from 12.1 mm to 33.5 mm (Figure 7). Mean length is 24.8 mm (SD=4.6). The smallest specimen has unopened gonopores and therefore can be considered to be a juvenile. Gonopores open between 12 mm and 17.7 mm, the next largest specimen being 17.7 mm in test length, having fully opened gonopores.

Of the characters measured on the aboral surface of the test, significant ontogenetic changes occur in the width of ambulacrum III, the length of the

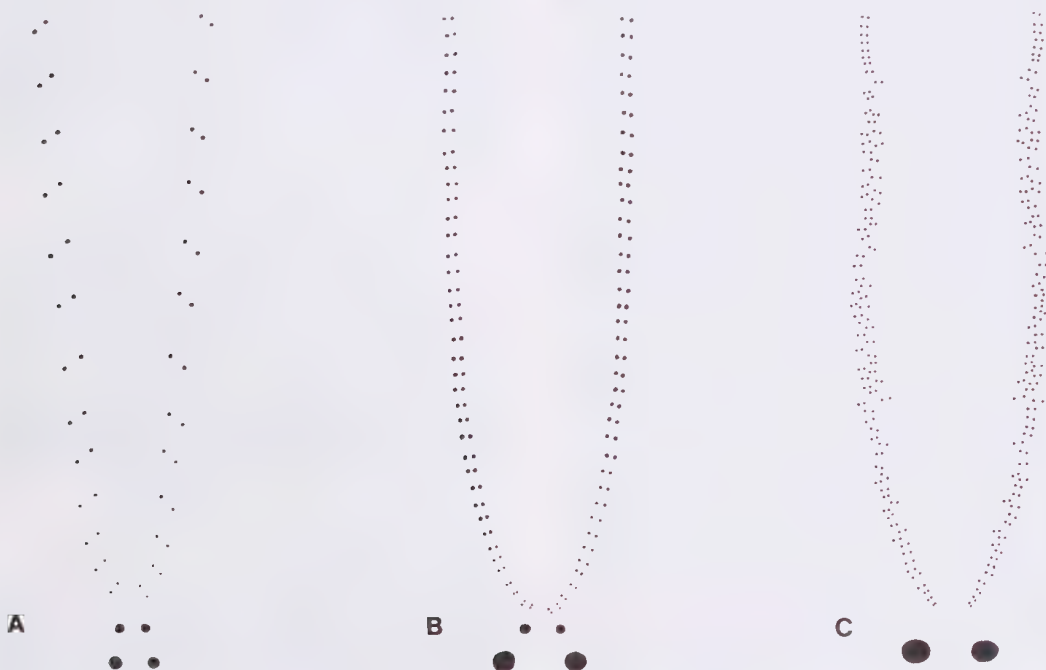


Figure 2 Arrangement of pore pairs in ambulacrum III aborally in the three subgenera of *Schizaster*: A, *S. (Paraster)*; B, *S. (Schizaster)*; C, *S. (Ova)*.

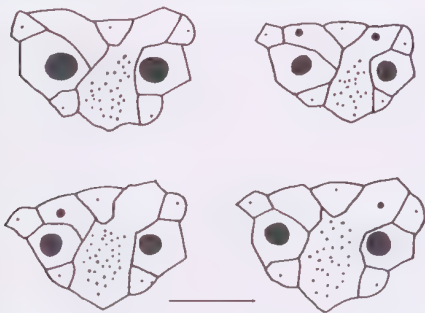


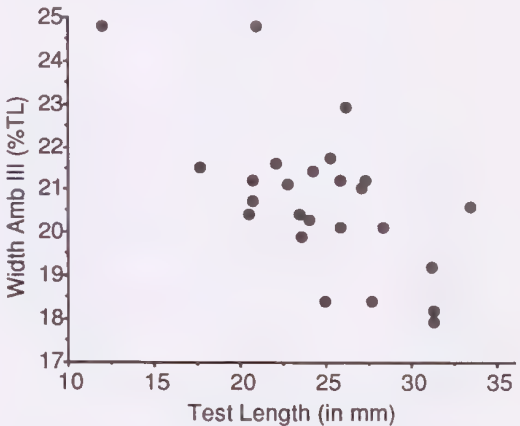
Figure 3 Variation in gonopore number in four adult specimens of *Schizaster* (*Schizaster*) *compactus* showing individuals with either two, three of four gonopores. In those specimens with three gonopores, the anterior gonopore may be either gonopore 2 or 3. Bar represents 1 mm.

posterior petals and the number of pore pairs in the ambulacra. As the test increases in size ambulacrum III becomes relatively narrower (Figure 4A), the width being 24.8%TL in the smallest specimen, decreasing to 18–19%TL in the largest specimens. A similar relative decrease in the width of ambulacrum III adorally was recorded in *Schizaster* (*Ova*) *myorensis* by McNamara and Philip (1980a, figure 6D). Ambulacrum III also shows a progressive increase in number of pore pairs throughout ontogeny, from 18 in each row in the smallest specimen to a maximum of 38 in the largest specimens (Figure 5C). However, this is not achieved by a lengthening of ambulacrum III and a posterior migration of the apical system, which is the situation in *Schizaster* (*Ova*) *myorensis*, rather the rate of pore pair production within the ambulacrum would have been greater during ontogeny.

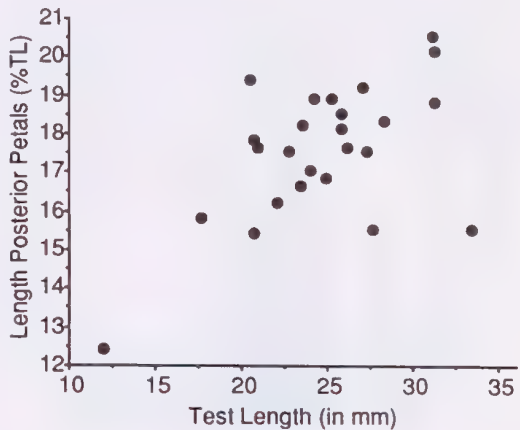
Of the other ambulacral characters, the only other to show significant shape changes are the posterior petals, which show a slight relative increase in length (from about 14%TL to almost 20%TL) (Figure 4B). This length increase coincides with the increase in number of pore pairs from eight to an average of 17 in the largest specimens (Figure 5A). The anterior petals similarly show an increase in the number of pore pairs in each row, from 17 to 30 (Figure 5B). This persistent production of pore pairs throughout ontogeny also occurs in *S. (Ova) myorensis* (McNamara and Philip 1980a). Although there is a slight increase in length of the anterior petals during ontogeny, it is highly variable (see below). There appears to be no correlation between those individuals with longer anterior petals and a greater number of pore pairs. This implies that the pore pairs are relatively more closely packed in larger individuals. Petal width, position of the apical system, and test height and length all show little or no ontogenetic variation. This is in contrast

to the situation in *S. (Ova) myorensis*, in which the test shape changes markedly during growth, becoming both relatively flatter and narrower (McNamara and Philip 1980a), and the apical system migrates posteriorly.

Mortensen (1951, p.222) observed that the three specimens of *S. (Schizaster) compactus* at his disposal, which were twice the size of Koehler's specimens, showed a more prominent development of the keel in interambulacrum 5 aborally. The Western Australian material similarly shows the adult specimens to have a more pronounced keel than the small juvenile (Figures 1C,F).



A



B

Figure 4 Plots of, A, width of ambulacrum III and B, length of posterior petals, expressed as percentages of test length against test length for *Schizaster* (*Schizaster*) *compactus*.

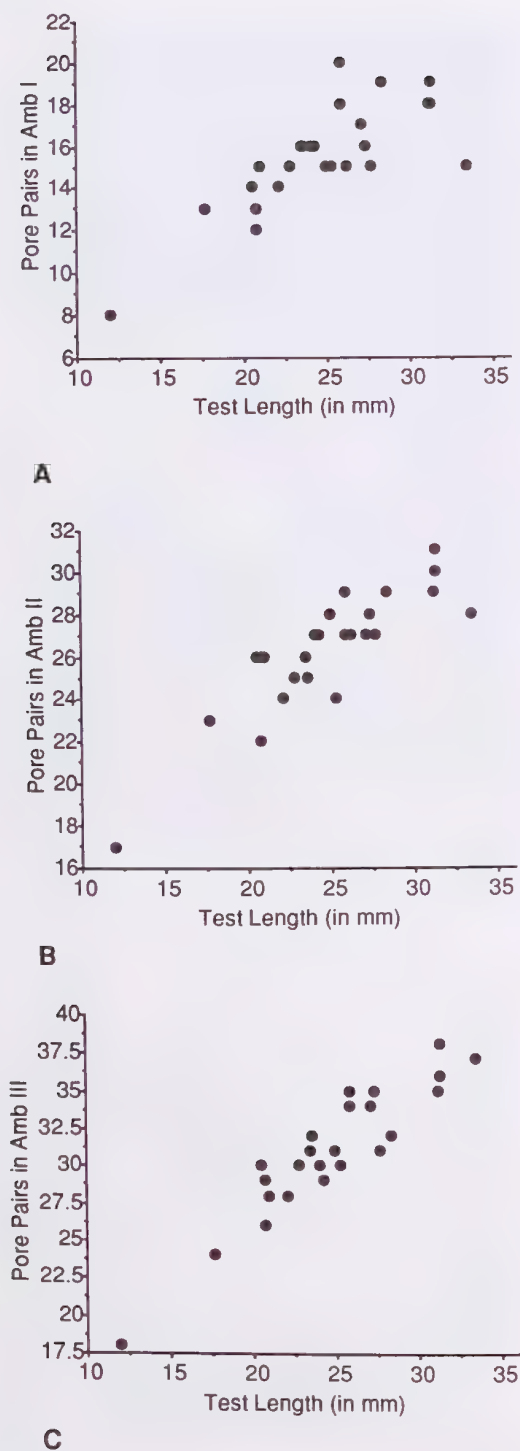


Figure 5 Plots of pore pairs in, A, ambulacrum I, B, ambulacrum II and, C, ambulacrum III aborally against test length for *Schizaster* (*Schizaster*) *compactus*.

On the adoral surface significant ontogenetic changes occur to the relative size and shape of the peristome and the periproct (Figure 6). The peristome becomes relatively smaller with growth, decreasing in width, from 20%TL to 16%TL (Figure 6A). Likewise, the peristome length (Figure 6B) decreases from 9%TL to a little over 4%TL. This relatively greater reduction in length, compared with width, arises, in part, from a relative increase in anterior growth of the labrum, which projects more across the peristome in larger specimens than in smaller ones (Figure 1). Unlike *S. (Ova) myorensis*, where the peristome becomes positioned relatively closer to the anterior ambitus through ontogeny, the peristome position in *S. (Schizaster) compactus* is highly variable (see below) and shows no such anterior trend. However, like *S. (Schizaster) compactus*, the peristome in *S. (Ova) myorensis* also becomes relatively smaller during ontogeny (McNamara and Philip 1980a).

The periproct likewise becomes relatively smaller during ontogeny. It is particularly wide in the juvenile specimen, being almost 15%TL, reducing during adult ontogeny from 12.5%TL to about 11%TL (Figure 6C). The slightly greater degree of reduction in relative length (Figure 6D), from 19%TL to 15%TL, compared with relative width, is reflected in a change in periproct shape, from subcircular to distinctly elongate. *S. (Ova) myorensis* similarly shows a decrease in periproct size during ontogeny. Other characters to undergo ontogenetic change are the anterior notch, which becomes relatively deeper and narrower (Figure 1), and the periplastral area which becomes relatively narrower (Figure 1).

Intraspecific variation

The most notably variable character in *S. (Schizaster) compactus* is the number of gonopores, which vary between two and four (Figure 3). Of the 27 specimens used in this study that had fully opened gonopores, 8 had two, 4 had three, and 15 had four. Thus, while Koehler (1914) defined the species, in part, on its possession of four gonopores, the examination of a larger population size than the two specimens Koehler used in his description, shows that only 55.6% of specimens had, in fact, four gonopores. A further 29.6% had three and 14.8% two (Figure 8). It would be interesting if sufficient numbers of specimens from the type locality in the Bay of Bengal ever became available, to see if similar variation exists in topotype material. The relative percentages of specimens with two, three and four gonopores show quite a close correspondence with the situation in *S. (Ova) myorensis* (Figure 8), where 14.3% had two gonopores, 11.5% had three and 74.2% four.

There is no correlation between number of

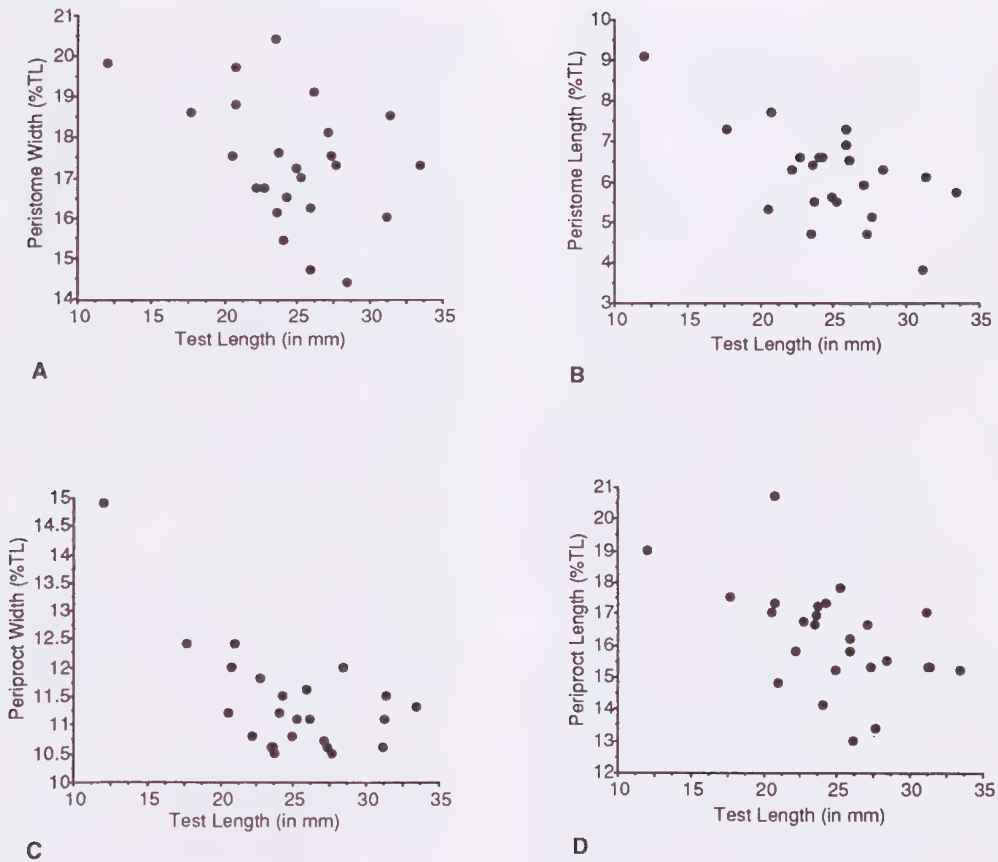


Figure 6 Plots of, A, peristome width, B, peristome length, C, periproct width and, D, periproct length, expressed as percentages of test length against test length for *Schizaster* (*Schizaster*) *compactus*.

gonopores and test size, the same proportion of large and small specimens having only two genital pores as have four gonopores. Of those that have three gonopores, the odd anterior pore may be either on the right side or the left side (that is, either gonopore 2 or 3). The anterior pair of pore pairs are consistently smaller than the posterior pair (Figure 6), a feature of the species noted by Mortensen (1951). They may be as large as about one third the diameter of the posterior gonopores, or as little as one tenth. The posterior pair open before the anterior pair and expand in area at a greater rate. The onset of opening of the anterior pair would seem to vary between individuals.

From a phylogenetic viewpoint these variations to the timing of opening of the anterior gonopores can be considered in a heterochronic context. The plesiomorphic condition within schizasterids is the possession of four open gonopores. In those individuals that produce only three, the delayed opening of the fourth gonopore occurs by postdisplacement, that is a delay in the time of opening of the gonopore (on the assumption that

test size is providing a reasonably valid metric for time). In those individuals that produce only two gonopores, there is also postdisplacement of the other gonopore. The three states therefore lie along a paedomorphocline (*sensu* McNamara 1982, 1990)

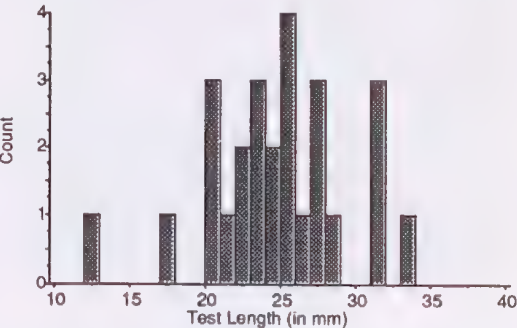


Figure 7 Histogram showing number of specimens in each 1 mm size class in the northwestern Australian population of *Schizaster* (*Schizaster*) *compactus*.

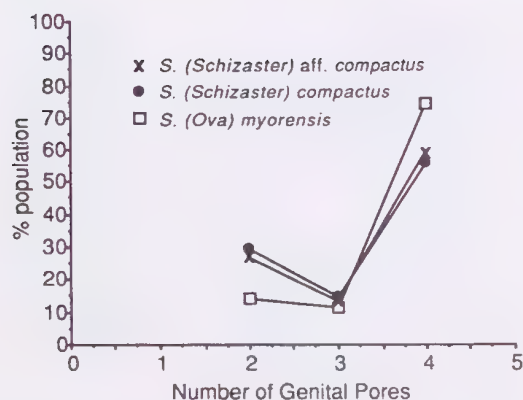


Figure 8 Similarity in percentage variation in gonopore number in the living species *Schizaster* (*Schizaster*) *compactus* and *Schizaster* (*Ova*) *myorensis* (data from McNamara and Philip 1980a), and the fossil species *Schizaster* (*Schizaster*) *aff. compactus* from the Middle Miocene Trealla Limestone, Gnargoo Range, Western Australia.

of four, three and two gonopores. This developmental flexibility in *S. (Schizaster) compactus* highlights the impracticality of using gonopore number as a generic or subgeneric diagnostic character. It may, however, serve as a useful character for the delineation of species, as the very flexible nature of the gonopore production may in itself be a species character.

The shape of the test shows a high degree of intraspecific variability. At mean test length, the test can vary in height between 64 and 72%TL ($n=22$). Similarly, the test width varies between 88 and 97%TL ($n=24$). *S. (Ova) myorensis* shows similar degrees of intraspecific variation in mature specimens (McNamara and Philip 1980a, figure 6A,B), but the ontogenetic variation that it displays does not occur in *S. (Schizaster) compactus*. On the aboral surface of the test the only character to show appreciable intraspecific variation is the position of the apical system. Specimens of mean test size show a variation in the distance of the apical system from the anterior ambitus of between 56 and 64%TL.

On the adoral surface the position of the peristome in relation to the anterior ambitus is highly variable, varying in mean specimens between 17 and 24%TL from the anterior ambitus. The maximum width of the plastron also shows a degree of variability, varying between 38 and 46%TL.

CONCLUSIONS

The ontogenetic development of *Schizaster* (*Schizaster*) *compactus* shows some similarities and some dissimilarities to the ontogeny of *Schizaster*

(*Ova*) *myorensis*. Both species share a narrowing of ambulacrum III adorally, an increase in number of pore pairs in the aboral petals and ambulacrum III, and relative decrease in size of the peristome and periproct. Other changes seen in *S. (Ova) myorensis*, but not observed in *S. (Schizaster) compactus*, are changes in shape of the test, the posterior migration of the apical system and increase in petal sinuosity. The greater extent of morphological development during ontogeny in *S. (Ova) myorensis* occurs because, compared with *S. (Schizaster) compactus*, it is a more peramorphic species, lying further along the peramorphocline between the "Paraster" morphotype and "Schizaster" morphotype (McNamara and Philip 1980b). The morphological changes that are common in the ontogenies of the species reflect changes during growth associated with feeding (peristome and periproct size), funnel construction (ambulacrum III size and pore pair number) and respiration (pore pair number in the petals).

The presence of variable pore pairs numbers in these two Australian species suggests the possibility that if large populations of other species of *Schizaster* from other regions are examined, the same effect will be seen. It is unlikely to be a purely Australian phenomenon. Neither is it likely to be a feature restricted to extant species. Indeed, an examination of fourteen specimens of an undescribed species of *Schizaster* from the Middle Miocene Trealla Limestone of the Gnargoo Range in the Carnarvon Basin, Western Australia, referred to as *S. (Schizaster) aff. compactus* by McNamara and Kendrick (1994), shows a similar variation of individuals with either two, three or four genital pores. Moreover, there is a startlingly similar ratio between the two species, with the Miocene species having 28.6% of specimens with two gonopores (compared with 29.6% in *S. compactus*), 14.3% with three (compared with 14.6%) and 57.1% with four (compared with 55.6%).

It has been demonstrated elsewhere (McNamara 1988, 1989, 1990) how important heterochrony has been to the evolution of spatangoid echinoids, and to *Schizaster* in particular (McNamara and Philip 1980b). Heterochrony has been shown to be more important as an evolutionary mechanism in those species that show both high degrees of ontogenetic and adult morphological variation. Many characters in *S. (Schizaster) compactus* fulfil these two criteria. If, as seems likely from other studies of phenotypic variation in species of *Schizaster* (McNamara and Philip 1980a), suites of characters covary, then perturbations to the characters that undergo morphological change during ontogeny are likely to have been an important factor in the evolution of the large number of species of *Schizaster* during the Tertiary.

The characterisation of species of *Schizaster*, and of echinoid species in general, needs to take into account both ontogenetic and general adult variation. The ontogenetic variation arises either from differentiation of novel features during growth (such as pore pairs or tubercles) or from growth of particular structures, such as coronal plates (McNamara 1988). Allometric growth of particular plates, either positive or negative, characterise species, but small variations to the allometries are the factors that produce adult phenotypic variation. The degree of variation itself can be a feature that characterises a species. High degrees of variation certainly make it harder to characterise species, but it is vital that both ontogenetic and adult phenotypic variation be taken into account when characterising species, either living or fossil.

ACKNOWLEDGEMENTS

I am grateful to Harry Butler and Bob Nunn for bringing the specimens to my attention. I wish to thank Kris Brimmell for the photographs. Thanks to Steve Donovan and Burt Carter for reviewing the manuscript and making helpful suggestions that tightened up the paper.

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Description of a new species of hardyhead, *Craterocephalus fistularis*, (Pisces: Atherinidae) from Irian Jaya

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Abstract – A new species of hardyhead, *Craterocephalus fistularis*, is described from Lake Kamakawaiar (Triton Lakes 3°47'S 134°14'E) in Irian Jaya. This fish is distinctive with upper and lower jaws slightly extended, giving the mouth a flute or funnel-like appearance. The scales covering body and head are crenulated. It has no external dentition; its teeth are small and not visible when the mouth is closed. Its lips are thick with a very thick labial ligament lying alongside the dentary. The new species is aligned with the *C. stercusmuscarum* group. Superficially, it resembles *Craterocephalus lacustris* but differs from that species and from all other members of the genus osteologically and meristically.

INTRODUCTION

Until about 1986, only 12 species of *Craterocephalus* (hardyheads) were known. In the next eight years extensive collecting and systematic work on this genus had, by 1990, increased the number to 24 with only one of these (*Craterocephalus nouhuysi*) being found in Irian Jaya. The new species, *Craterocephalus fistularis*, was collected from a lacustrine habitat, Lake Kamakawalar (3°47'S 134°14'E) in western Irian Jaya.

The genus *Craterocephalus* has been divided into three groups by Ivantsoff *et al.* (1987), Crowley and Ivantsoff (1988; 1992), and Crowley (1991). The external morphology and osteology align the new species with the *C. stercusmuscarum* group. The distinguishing external characters of this group include a relatively slender body (when compared with *C. eyresii* group) and thin body scales. The dark midlateral band running from snout to caudal peduncle, which is generally characteristic of the *C. stercusmuscarum* group, is, however, only faintly visible in the new species running from the pectoral fin origin to caudal peduncle. *Craterocephalus fistularis* shares with members of the *C. stercusmuscarum* group fused 5th ceratobranchial bones, urohyal with ventral pocket and wings, pectoral girdle with small scapular foramen and corocoid shelf present and well developed interdorsal pterygiophores (For detail see Crowley and Ivantsoff 1992).

MATERIALS AND METHODS

Two specimens were available for morphometric measurements and meristic counts. One specimen was cleared and stained for osteological analysis

after measurements and counts had been made. Clearing and staining followed the methods of Taylor (1967). Measurements and counts follow the methods of Ivantsoff *et al.* (1987). Results in Table 1 compare the new species with its potentially closest relative, *C. lacustris*, from Lake Kutubu in Papua New Guinea.

SYSTEMATICS

Craterocephalus fistularis sp. nov.

Figure 1

Holotype

MZB 6114 (76.6 mm SL) Lake Kamakawaiar, (3°47'S 134°14'E), Triton Lakes, Irian Jaya. Collected by Dr. G.R. Allen and D. Price, 14 May 1991. Seine in shallow water (0.5–1.5 m) along the eastern shore, near the southern tip of the lake.

Paratype

WAM P.30519–002 (58.5 mm SL) data as for holotype. This specimen was cleared and stained for osteological analysis

Diagnosis

Moderately robust freshwater fish, mouth small, gape very restricted. Labial ligament and lips very thick (Figure 2A). Lips with continuous flap at free edge. Gill rakers in lower gill arch (14–15) short and stumpy, with minute spinules. Transverse scales 8.5. Predorsal scales 22–23. Body scales crenulated and almost square (Figure 2E). Scales covering interopercle as far as vertical through anterior edge of orbit. Infraorbitals very broad

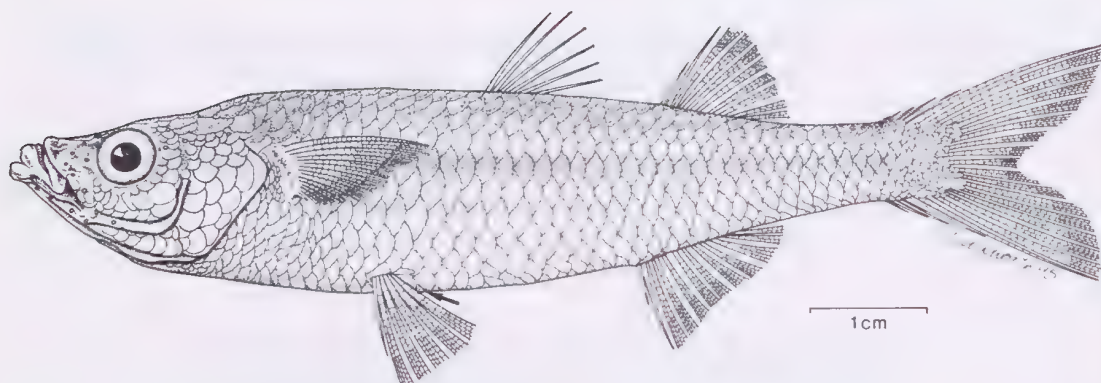


Figure 1 Holotype of *Craterocephalus fistularis* MZB 6114.

(Figure 2E). Large number of predorsal scales unique for this species. No other species of freshwater *Craterocephalus* has crenulated scales.

Description

Member of the *C. stercusmuscarum* group but with moderately deep body. Mouth in larger fish extended forward giving pipe or funnel-like appearance. Gape restricted by labial ligament more than half way along free edge of premaxilla (Figure 2A). Needle-like teeth on medial third of premaxilla and dentary; other bones of mouth edentulous. Scales on dorsum of head irregular, as far as vertical through anterior pupil of eye. Midlateral scales 37–38. Position of anus from 2 to 4 scales behind tips of pelvic fins; origin of first dorsal fin from 1 to 1.5 scales in front of tips of pectoral fins. For details of all measurements and counts and a comparison with *C. lacustris* see Table 1.

Osteological characters

Dorsal process of premaxilla long, reaching into interorbital space. Lateral ramus of premaxilla not reaching to vertical through anterior edge of orbit. Coronoid process of dentary highly elevated, 5th ceratobranchial bones fused. Scapular foramen small; corocoid shelf large. Anal plate not extended forward as in most other members of *C. stercusmuscarum* group. Differs from *C. lacustris* and from all other species of *Craterocephalus* by a combination of the following: Shape and extent of labial ligament (Figure 2A), shape of premaxilla and maxilla (Figures 2B, 2C), coronoid process of dentary rounded anteriorly (Figure 2D), width of infraorbital bones (Figure 2E). The new species also differs from other members of the *C. stercusmuscarum* group in: shape of basihyal, epibranchials, hyomandibular metapterygoid and interdorsal pterygiophores. In other species of *C. stercusmuscarum* group, basihyal bone slender with short associated cartilage; in *C. fistularis* basihyal

bone robust with well defined triangular shelf on ventral aspect; associated cartilage reduced to small pad. Epibranchial bones of *C. fistularis* relatively robust (slender in other species); *C. fistularis* hyomandibular with distinct posterior projection for articulation with opercle (no distinct projection in other species). Metapterygoid small in *C. fistularis*; medium to large in other *C. stercusmuscarum* group species. *Craterocephalus fistularis*, interdorsal pterygiophores large with well developed descending process; in all other *Craterocephalus* species interdorsal pterygiophores small, vestigial or absent.

Colour

Preserved specimens pale yellowish buff; paler towards abdomen. Faint midlateral band from origin of pectoral fin to base caudal fin. Midlateral band initially very thin line to vertical through origin of first dorsal fin, then slightly wider (less than scale width). Midlateral band absent from snout through eye. Melanophores above midlateral band faint, reticulate pattern not apparent. Melanophores lacking on abdomen. Dorsum of head dusky. Snout and lips peppered with melanophores. Eyes silvery black. Fins clear with few melanophores along rays.

Etymology

fistularis from the Latin for pipe or flute, referring to the shape of the mouth.

Distribution

This new species is presently known only from Lake Kamakawalar, Irian Jaya.

Discussion

Craterocephalus fistularis shares with the *C. stercusmuscarum* group all of the osteological characters given above. These characters can be used to define the group and to differentiate members of the group from members of both the

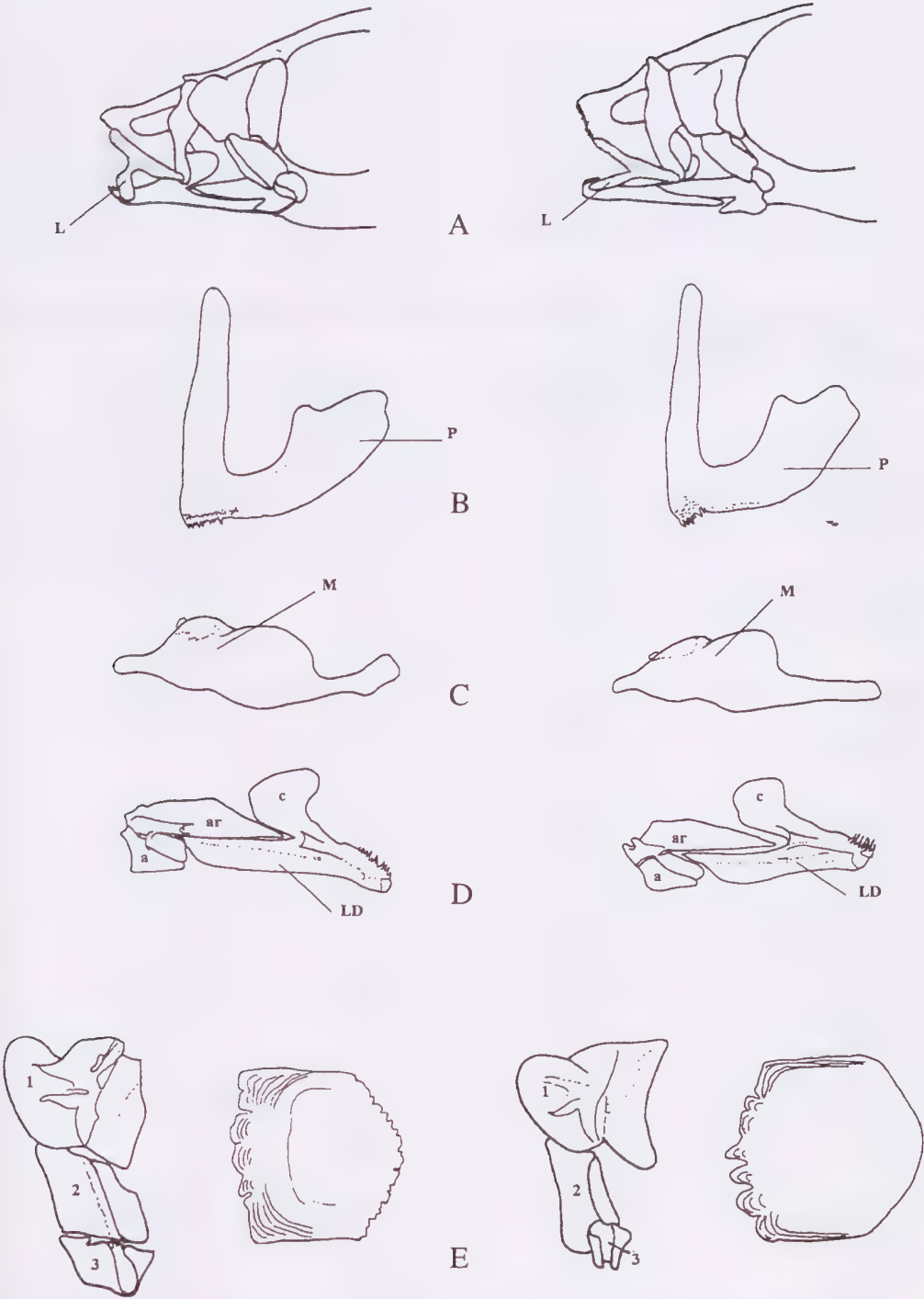


Figure 2 A, Lateral view of mouthparts and labial ligament (L) in *C. fistularis* (left) and *C. lacustris* (right); B, Lateral view of premaxilla (P); *C. fistularis* (left) and *C. lacustris* (right); C, Lateral view of maxilla (M); *C. fistularis* (left) and *C. lacustris* (right); D, Medial view of left dentary (LD) showing: a, angular; ar, articular; c, coronoid process; *C. fistularis* (left) and *C. lacustris* (right); E, Infraorbitals 1-3 (1, 1st infraorbital; 2, 2nd infraorbital; 3, 3rd infraorbital) and scale of *C. fistularis* (left) and *C. lacustris* (right).

C. eyresii group and the *C. honoriae* (marine) group (Crowley and Ivantsoff 1992).

Although members of the *C. stercusmuscarum* group are genetically and morphologically very similar, the new species has a number of unique characters, in particular the crenulate scales, number of predorsal scales and extent of labial ligament. Despite these characters, *Craterocephalus fistularis*, is most closely related to *C. lacustris* on the basis of osteological and morphological characters. *Craterocephalus lacustris* is a lacustrine

hardyhead species found in Lake Kutubu, Papua New Guinea. Crowley *et al.* (1991) have shown how closely related genetically are the other members of the *C. stercusmuscarum* group, from the southern drainages of Papua New Guinea and Irian Jaya. However, it was not possible to find the genetic affinities of the new species as no fresh or frozen material was available for electrophoretic analysis.

The number of freshwater hardyhead species of the *C. stercusmuscarum* group now known from Papua New Guinea and Irian Jaya, is the same as

Table 1 Comparison of holotype and paratype of *Craterocephalus fistularis* with *C. lacustris*. Last double ray of second dorsal and anal fins counted as one.

Character	<i>C. fistularis</i> holotype	<i>C. fistularis</i> paratype	<i>C. lacustris</i> (n=42)
In SL (standard length)	3.2	3.3	3.4(3.2–3.8)
Head Pectoral length	5.1	7.2	6.4(5.1–9.4)
Max. body depth	4.2	4.4	4.6(3.5–6.0)
Min body depth	10.7	11.2	11.7(10.6–12.9)
Pec/anus	2.8	3.1	3.4(3.0–4.0)
SnOD1	1.9	1.9	2.1(2.0–2.2)
SnOD2	1.4	1.4	1.4(1.4–1.5)
SnOV	2.2	2.3	2.3(2.2–2.4)
SnTV	1.7	1.7	1.7(1.6–1.8)
SnOA	1.4	1.4	1.5(1.4–1.6)
SnTA	1.2	1.3	1.2(1.0–1.5)
In Head			
Eye	4.1	3.5	3.4(2.9–5.0)
Interorbital	2.9	3.1	3.2(2.9–3.6)
Postorbital	2.3	2.4	2.3(2.0–2.7)
In Eye			
Snout	0.7	1.0	1.2(0.7–1.5)
Premaxilla	0.8	1.1	1.1(0.7–1.4)
Lips in premaxilla	1.7	1.6	2.0(1.5–2.4)
Premax. process	1.0	1.4	1.3(0.8–1.9)
Meristics			
Scales and vertebrae			
Midlateral	38	37	34.3(32–38)
Transverse	8.5	8.5	7.3(6–8)
Predorsal	23	22	13.8(11–18)
Interdorsal	7	8	7.4(6–9)
Vertebrae	–	36	36.5(35–39)
Finrays			
First dorsal	6	5	7.1(5–8)
Second dorsal	Ii 7	Ii 6	Ii 6–8
Anal	Ii 9	Ii 8	Ii 7–9
Pectoral	Ii 13	Ii 13	Ii 11–15
Other			
Gill rakers	14	15	11.7(10–13)
Posit anus	B4	B1.5	F1(F0–2)
OD1–TV	F1	F1.5	F5.2(F3–7.5)
OD1–TPec	B2	B2	B0.8(F1–B3)
OV–TPec	F3	F2.5	F1.5(F0–3)

Abbreviations: Pec/anus – length from origin of pectoral fin to anus; Posit. anus – position of anus in relation to tips of ventral fins; OD – origin of first dorsal fin; OD2 – origin of second dorsal fin; OV – origin of ventral fin; Sn – snout; OA – origin of anal fin; TA point of insertion of last double ray of anal fin; TV – tips of ventral fins; TPec – tips of pectoral fins; F or B – number of scales in front of or behind reference point

in the whole Australian mainland – that is five species in each country. However, there are greater differences between the new species *C. fistularis* (see above) and the other members of the *C. stercusmuscarum* group from Papua New Guinea/Irian Jaya (Crowley and Ivantsoff 1992) than there are between all Australian species of this group. The difference might be attributed to longer separation from the main *C. stercusmuscarum* ancestor (Crowley *et al.* 1991) or to increased ecological pressures. Until electrophoretic studies can be carried out on the new fish to assess its genetic relationships with other members of the group, the answer to the question of its marked differences must remain unknown.

ACKNOWLEDGEMENTS

We would like to thank Ms Barbara Duckworth for her line drawing of the holotype. Ms Jenny Norman was most helpful with the photographic preparation of the drawings. This is publication No.178 of the Research Unit for Biodiversity and Bioresources within the School of Biological Sciences at Macquarie University.

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Manuscript received 24 April 1995; accepted 17 July 1995.

Acanthodian dental elements from the Trundle beds (Lower Devonian) of New South Wales

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Abstract – Acanthodian dental elements from the Trundle beds (Lochkovian-Pragian) of central New South Wales include dentigerous jaw bone fragments, tooth whorls, single teeth, and dentition cones *sensu* Valiukevičius. Among acanthodians, only members of the Order Ischnacanthida possess an equivalent range of dental elements. Comparisons suggest that most of the Trundle beds elements belong to an ischnacanthid taxon with close affinity to *Poracanthodes*. Some other elements, distinctive tooth whorls including a type not previously described, possibly belong to a species with dentition that matches no known climatiid or ischnacanthid.

INTRODUCTION

The Class Acanthodii, as defined by recent workers (e.g., Denison 1979; Long 1986), has two orders which possessed teeth – the Climatiida and the Ischnacanthida. Amongst the climatiids, only fish of the family Climatiidae had teeth, comprising rows of tooth whorls. The Ischnacanthida are distinguished from other acanthodians by possessing dentigerous jaw bones, or gnathals, on both upper and lower jaws.

Acanthodian dental elements, including dentigerous jaw bone fragments, tooth whorls, isolated single teeth and dentition cones (*sensu* Valiukevičius 1992) occur in shallow water, marine limestones from the upper Lochkovian/lower Pragian Trundle beds (informal geological name; Pickett 1992; Pickett and McClatchie 1991) of central New South Wales (Figure 1). Isolated scales of at least four acanthodian species (Burrow in press) have been reported from these same beds. This material comprises rare scales of the climatiid *Nostolepis striata* and *Machaeracanthus* sp. (*Acanthodii incertae sedis*), and abundant scales of a new species (Burrow in press) and "*Nostolepis*" *guangxiensis* Wang, both of which might be ischnacanthids.

Few systematic descriptions of Australian Early Devonian acanthodian microremains have been published; Gross (1971a) described a small collection of acanthodian scales from Wilson's Cliffs, Western Australia, but the paucity and poor preservation of the material precluded classifying the scales. Long (1986) described small ischnacanthid gnathal bones of two types from the Emsian Spirifer yassensis and Cavan Bluff Limestones, Murrumbidgee Group, near Taemas, New South Wales, and from the uppermost Emsian

Rocky Camp member, Murrindal Limestone, Buchan Group of Victoria. He assigned the bones to two separate genera, *Taemasacanthus* and *Rockycampacanthus* (Figure 2A–C) respectively. Turner (e.g., 1991) has recorded many occurrences of acanthodian scales, and has also reported occurrences of dental elements (e.g., Turner 1991, plate 2, fig. D).

Worldwide, a number of ischnacanthid taxa have been described based on isolated dentigerous jaw bones; only a small number (*Ischnacanthus gracilis*, *Uraniacanthus spinosus* and *Poracanthodes menneri*) are based on descriptions of articulated fish. Assigning the gnathal bones to the upper or lower jaw is often not possible, as only rarely is the posterior end preserved with the dentigerous area. Moreover, in the taxa based on articulated specimens, the upper and lower dentigerous zones are identical.

The present paper describes the acanthodian dental elements found in the Trundle beds samples, including two previously undescribed elements – a denticulated plate plus toothwhorl, and the posterior end of a probable upper jaw gnathal. An attempt is made to elucidate the dental patterns of the acanthodian fish from which the elements derive, and the affinities of these taxa are discussed.

MATERIAL

The specimens described in this study are from limestone samples collected and treated with acetic acid by Dr John Pickett (Geological Survey of New South Wales), and subsequently picked for microvertebrates by Dr Susan Turner (Queensland Museum) and the author. The samples are from

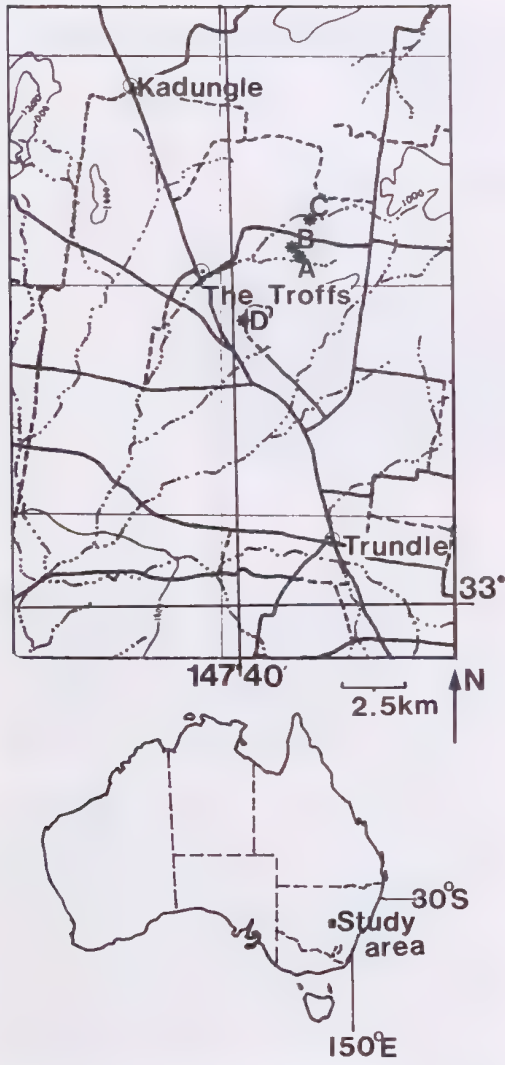


Figure 1 Location of sites C607, C661, C662 and C665 of the Trundle beds; map adapted from Australian Topographical Map Series 1:250000 Narromine. Site C607(=A): 6 km E of The Troffs railway station, GR 573500 941800; site C661(=B): tank S of "The Troffs" station, GR 573000 942000; site C662(=C): Dam at foot of hills of volcanics, "The Troffs" station, GR 575000 943000; site C665(=D): 3 km SE of The Troffs railway station, GR 572000 938000.

sites C607, C661, C662 and C665 in the Trundle beds of central New South Wales of Early Devonian age (Lochkovian; *pesavis* zone) (Table 1). Site and specimen numbers were provided by Dr Pickett; MMMC = Fossil collection of the Mineralogical and Mining Museum, Sydney.

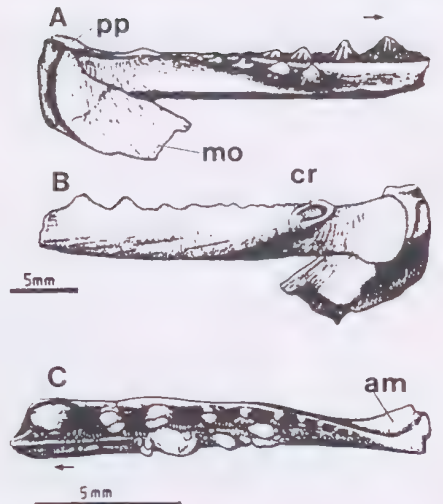


Figure 2 Gnathal bones of other Australian ischnacanthids, after Long 1986, figs 3A,C and B. A, *Taemasacanthus* lower jaw, medial view; B, same jaw, lateral view; C, *Rockycampacanthus* lower jaw, occlusal view. am = attachment area for adductor mandibulae, cr = circular ridge, mo = Meckelian ossification, pp = posterodorsal process of lower jaw. Scale bar = 5 mm; arrows indicate rostral direction.

DESCRIPTIONS

Class Acanthodii

Order Ischnacanthida Berg, 1940

Ischnacanthid fam., gen. et sp. indet.

Represented by 12 dentigerous jaw fragments, 21 tooth whorls, 14 isolated teeth, and 15 dentition cones (Table 1). In the following account the most

Table 1 Number of dental elements present in each Trundle beds sample.

	C607	C661	C662	C665
Anterior jaw fragment	3	4	—	—
Mid jaw fragment	—	3	—	—
Posterior jaw fragment	—	2	—	—
Symmetrical tooth whorl	5	8	—	—
Single tooth	7	5	2	—
Dentition cone I	5	2	—	—
Dentition cone II	5	2	—	1
Asymmetrical tooth whorl	1	—	—	—
Denticulated plate plus tooth whorl	1	3	2	1

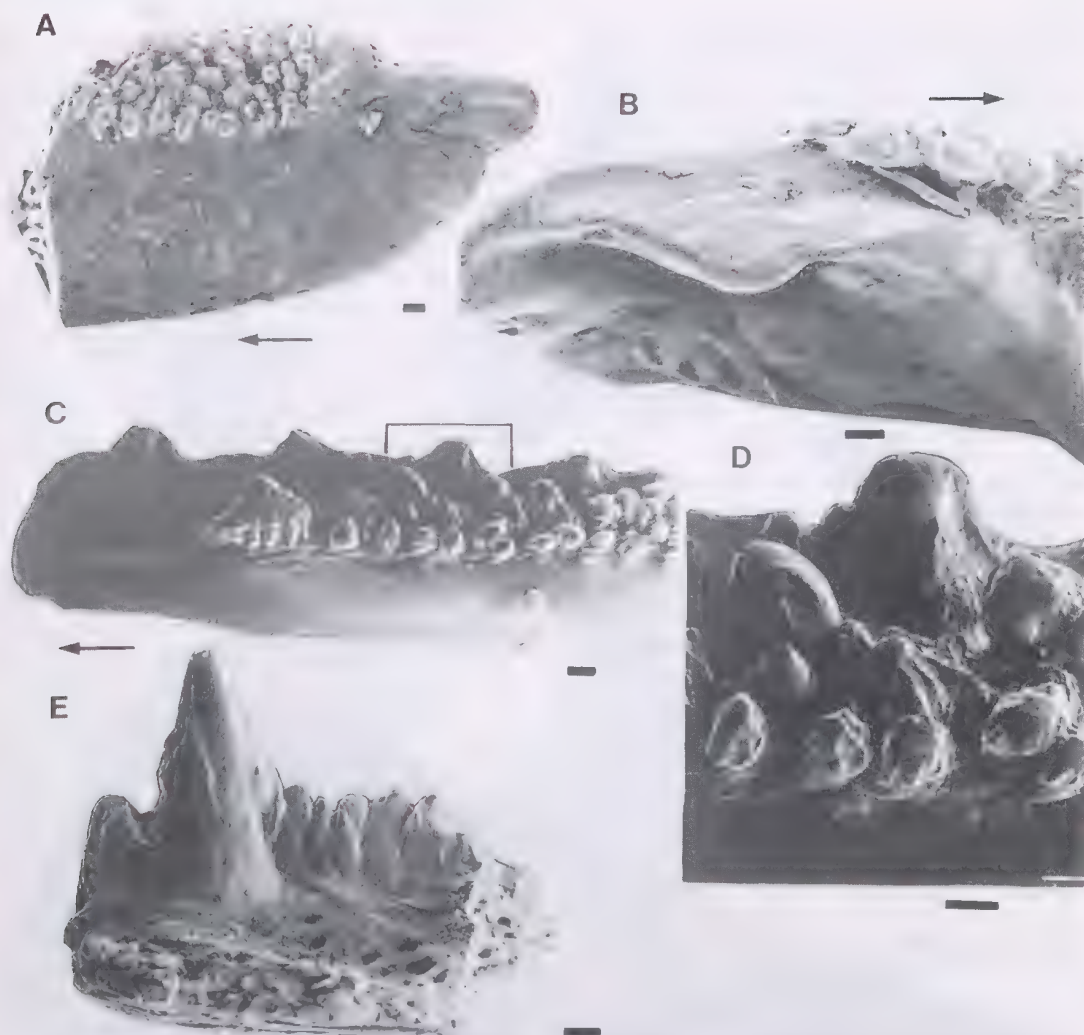


Figure 3 Dentigerous jawbone fragments from Trundle beds, central New South Wales. A,B, posterior ?upper jaw fragment MMMC02280: A, lateral view and B, occlusal/medial view; C,D, mid jaw fragment MMMC02279: C, medial view, D, close-up of tubercles on medial ridge in C; E, anterior jaw fragment MMMC02278. Scale bars = 0.1 mm; arrows indicate rostral direction; Figures C,D,E are SEM photographs of uncoated specimens.

complete or best preserved specimen of each type is first described and figured, followed by brief details of other specimens of the same type.

Posterior jaw bone fragment (Figure 3A,B)

This fragment (MMMC02280) is 2.4 mm long, 1.5 mm deep and 1.0 mm wide at the anterior, broken edge. The top edge of the bone is narrow, and the anterior section bears small rounded denticles. A small, flat, ledge-like process juts out medially towards the posterior end; the end of the bone then curves gently round to the bottom edge. On the medial side, a ridge starts at the anterior edge of the ledge-like process, increasing in size as it

sweeps down and forward to form the medial side of the basal concavity for the jaw cartilage. The lateral side of the bone is slightly convex top to bottom, and bears small, rounded denticles in the upper half.

A second similar fragment is 3.0 mm long, with the same shape and relative robustness, and is contralateral to the illustrated jaw fragment.

Dentigerous jaw bone (Figure 3C,D)

The best preserved jaw bone fragment (MMMC02279) is 4.0 mm long, 0.7 mm wide posteriorly and increasing to 1.0 mm wide anteriorly, and is approximately 1.0 mm deep. The

anterior and posterior ends are broken; the base is transversely concave. The main tooth row extends along the lateral edge of the occlusal surface of the jawbone, and comprises a series of five multicuspidate teeth which increase in size and number of side cusps posterior to anterior. The main cusps are sub-triangular in parabasal section, with the 'angles' positioned anteriorly, posteriorly and medially. The posterior teeth are low and worn, with side cusps barely discernible. The anterior teeth are formed by a main cusp and one medial, three anterior and two or three posterior cusps. The main tooth row is separated by a deep channel from a medial tuberculated ridge, which bears approximately 40 irregularly clustered tubercles varying from less than 0.1 mm wide to 0.5 mm wide at the base, and with from five to 13 or more radiating ribs. They have worn, rounded apices, and are directed medially or vertically. The ridge diminishes in height from 0.8 mm posteriorly to 0.4 mm at the anterior limit of the tubercles.

The other two fragments are shorter, but of comparable depth and robustness. If all three fragments had originally been positioned on the lower jaw, two are from the left side and one from the right side. A vertical, transverse, ground thin section was made of one of the fragments (MMMC02276, Figure 6A). Wide, vascular canals extend throughout the bone base, and up into the main cusp. Denteons surround some of the canals, with bone cell lacunae between the denteons. Orthodentine tubules are present in the large tubercle of the medial ridge, and in the upper section of the main tooth cusp.

Anterior jaw fragment (Figure 3E)

This fragment (MMMC02278) is 1.5 mm long, and has one almost complete tooth 'group' (i.e., a main cusp plus side cusps) with one large cusp, three posterior side cusps and two anterior side cusps. The distal surface of the jaw fragment is flat. The posterior cusps are overlapped laterally by the anterior cusps of the next tooth group. The main cusp is 0.6 mm high with a sub-triangular parabasal section, and the smaller cusps are about 0.15 mm high, and laterally flattened with an elliptical parabasal section.

The other six fragments range from 1.4 to 2.0 mm long, including a very robust fragment with a main cusp that is 2.0 mm high. It is not possible to determine the original orientation of most of the fragments. Figure 6B is of a vertical, longitudinal, ground thin section of a fragment (MMMC02274) with one main cusp and three side cusps, and illustrates the highly vascular structure of the bone base and main cusp. The secondary cusps are less vascular, and are formed of a relatively dense, dentinous tissue. Separation between the lateral ridge tissue and the central tissue of the main cusp is clearly delineated.

Symmetrical tooth whorl (Figure 4A)

In crown view, the base of this specimen (MMMC02249) is sub-triangular in outline, being 0.7 mm wide posteriorly and narrowing to a rounded point anteriorly. The base is arched, and is concave anterior to posterior. The crown has four tooth rows, with the cusps decreasing in size to the front. Each row has a prominent central cusp, the largest being 0.5 mm high; on each side there are up to four subsidiary cusps, approximately a quarter of the height of the central cusp. The central, or main, cusps have sub-triangular parabasal sections, with the angles pointing anteriorly and laterally. The three ridges which contribute to this triangular cross section differ in appearance from the central cusp area, being coloured white whereas the rest of the cusp is amber.

The other 12 tooth whorls of this type range greatly in size and relative robustness of the cusps and base: the smallest is 0.4 mm long and high, while the largest is over 2.0 mm long with a central cusp nearly 2.0 mm high. The tooth whorls comprise from three to six tooth rows; on some, the main cusp is only about twice as high as the side cusps, while on others the main cusp is up to four times as high (e.g., toothwhorl MMMC02256, Figure 4B,C). The number of cusps per tooth row is also variable, with from two to six or more side cusps. The number of side cusps varies independently of the size of the tooth whorl. One of the tooth whorls (MMMC01962, Figure 4G), while having the same generalized form as the other tooth whorls in this category, has a 'segmented' base corresponding to its tooth rows. In Figure 6C, a vertical, rostro-caudal, ground thin section of tooth whorl MMMC02275, central 'pulp canals' of the main tooth cusps are clearly visible, with fine orthodentine tubules radiating obliquely from them. Bone cell lacunae appear to be concentrated in the bone base.

Single tooth (Figure 5A)

The slightly recurved tooth (MMMC02277) is 0.7 mm high and has a base diameter of 0.3 mm. It has a narrow conical shape, with a hollow base of circular cross section, and a rounded apex. The tooth has a ring of small cusps approximately 0.4 mm from the tip, and has the dull appearance of bone below this ring, whereas it is shiny and dentinous above it.

The other 13 teeth are all of a similar size and shape.

Dentition cone, type I (Figure 5B)

This element (MMMC02252) is a hollow, thin-walled, bisymmetrical cone, 1.0 mm high, with a base diameter of 0.35 mm. It is characterised by an apex to base line of oblique spiny denticles. The



Figure 4 Tooth whorls from Trundle beds, central New South Wales. A, occlusal view, ischnacanthid symphyseal tooth whorl MMMC02249; B,C, symphyseal tooth whorl MMMC02256, with main central cusp ca. four times as high as side cusps: B, antero-lateral view, showing arched base, and C, occluso-lateral view; D, lateral view, and E, occlusal view of ?mouth cavity multiple tooth whorl MMMC02250; F, lateral view of denticulated plate plus tooth whorl MMMC02251; G, occluso-lateral view of symmetrical tooth whorl MMMC01962. dp = denticulated plate, tr = tooth rows, tw = tooth whorl. Scale bars = 0.1 mm; arrow indicates rostral direction; Figures A,D,E are SEM photographs of uncoated specimens.



Figure 5 Single tooth and tooth-like cones from the Trundle beds, central New South Wales. A, single tooth MMMC02277; B, tooth-like cone type I MMMC02252; C, tooth-like cone type II MMMC02268. Scale bars = 0.1 mm; A is an SEM photograph of an uncoated specimen.

latter appear to consist of a row of tooth-like processes interspersed with smaller, irregularly arranged processes/cusplets. The arrangement is reminiscent of that of the main cusp row of the dentigerous jaw bones.

The other six cones of this type are of a similar size and shape.

Dentition cone, type II (Figure 5C)

This cone (MMMC02268) is more robust than the previous type, with thicker walls and oblique denticles scattered over the cone surface. The main cone body is formed of bone, while the denticles are shiny and probably dentinous.

The other six cones range from 0.8 to 2.0 mm high.

Class *Acanthodii incertae sedis*

Acanthodii gen. et sp. indet.

Asymmetrical multiple tooth whorl (Figure 4D,E)

This incomplete element (MMMC02250) is 0.9 mm long and 0.4 mm wide centrally, and has an arched base, bearing radiating whorls of teeth. The crown comprises two apparently complete whorls, each with at least six teeth or tooth rows. The teeth increase gradually in height from less than 0.1 mm at the front to as much as 0.6 mm at the rear. The largest tooth row of the best-developed whorl has the largest central cusp, which has two side cusps about 0.15 mm high. The cusps are sub-circular in parabasal section. Side cusps are poorly developed

or absent on most teeth. Adjacent to the anterior section of this whorl are two broken teeth which appear to be part of a third whorl.

Denticulated plate with tooth whorl (Figure 4F)

This asymmetrical element (MMMC02251) is 1.1 mm long and 0.3 mm wide. The posterior portion has a similar form to that of typical tooth whorls – i.e., a concave base, and tooth rows with a large central cusp and smaller side cusps. The whorl is skewed relative to the anterior base plate, which is elongated and flat. Its crown has worn, irregularly shaped cusps or tubercles. The thin lateral edges of the plate are also tuberculated.

The other six plates are of a similar size and pattern; three have a tooth whorl skewed right relative to the plane of the plate, and three are skewed to the left (if all were originally positioned in either upper or lower jaws). Plate MMMC02205 (Figure 6D) was sectioned longitudinally; unfortunately, preservation was poor, and most histological detail is obscure (Figure 6E).

DISCUSSION

Early ischnacanthids possessed a wide range of dental elements, as evidenced by those fish that have been found as articulated specimens, and by the detailed studies of microremains by Gross (e.g., 1957, 1967, 1971b). In the following paragraphs, the new specimens are compared with those previously described, to determine the possible positions and affinities of the dental elements.

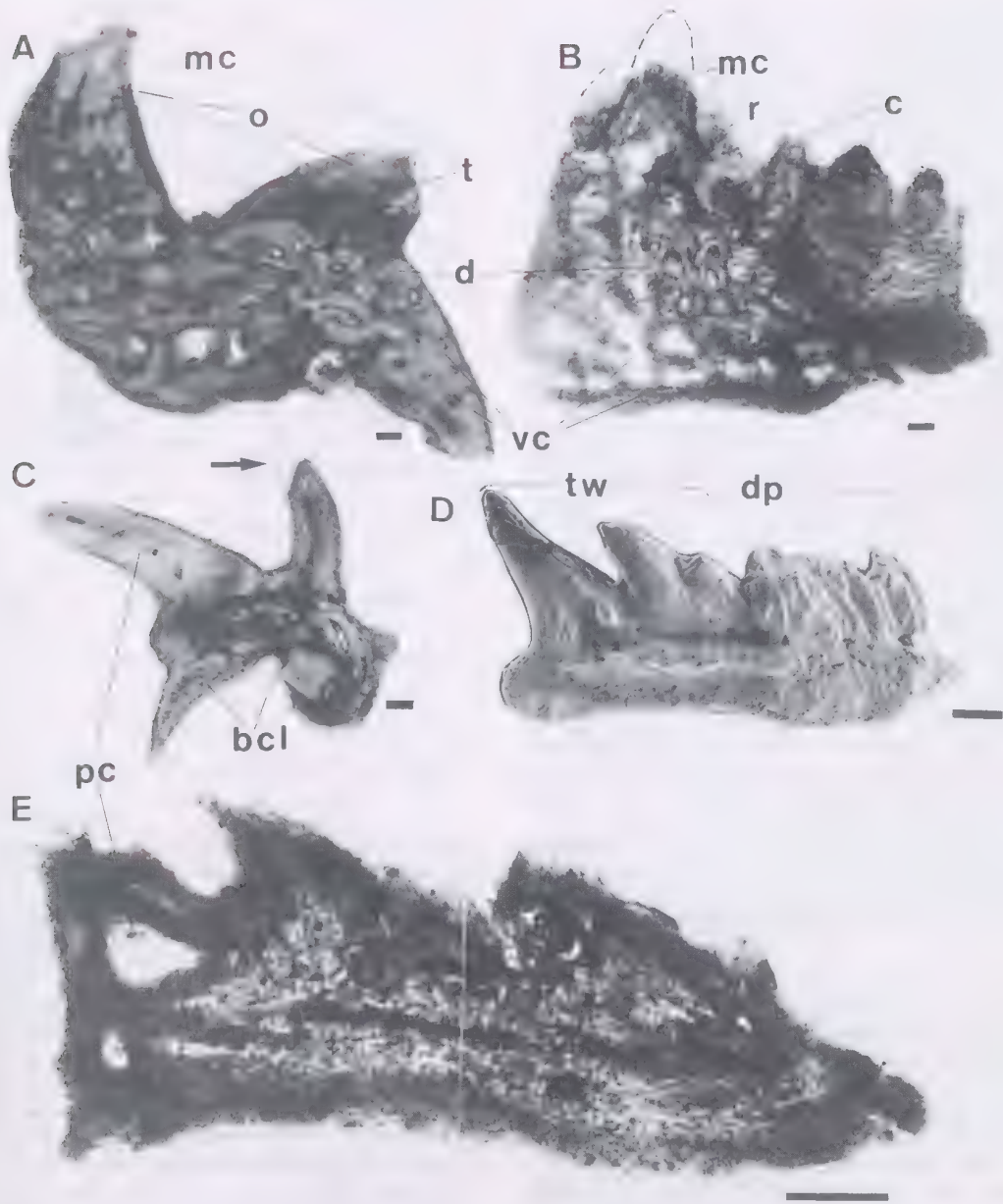


Figure 6 Ground thin sections of dental elements from the Trundle beds, central New South Wales. A, vertical transverse section of dentigerous jaw bone fragment MMMC02276; B, vertical longitudinal section through the main cusp and three side cusps of jaw bone fragment MMMC02274; C, vertical longitudinal section of symphyseal tooth whorl MMMC02275; D, SEM photograph of uncoated denticulated plate with tooth whorl MMMC02205; E, longitudinal section of plate in D. bcl = bone cell lacunae, c = side or secondary cusps, d = denteon, dp = denticulated plate, mc = main cusp, o = orthodentine, pc = 'pulp' canal, r = lateral ridge of main cusp, t = tubercle of medial ridge, tw = tooth whorl, vc = vascular canal. Scale bars = 0.1 mm; arrow indicates rostral direction.

Gnathal bones

Ischnacanthid dentigerous jaw bones, and fragments thereof, are often readily recognizable by their characteristic latero-medially arched, basal concavity, which straddled the jaw cartilages. Ischnacanthids had the simplest jaw joint of all acanthodians, with a single simple articulation (Long 1986). In *Taemasacanthus* the lower jaw articulation area is on the end of a "meckelian ossification" (Long 1986, figure 3a), rather than the dentigerous jaw bone, and the posterior margin of the latter is splayed outwards. The posterior margins of lower jaw gnathals of *Persacanthus* (both in the holotype material, and a jaw described by Reed 1986), *Rockycampacanthus* (Long 1986) and *Atopacanthus* (Ørvig 1957, plate 2, figure 5) have a similar shape, and also lack any sign of an articulation area. Posterior jaw bone fragments comparable to those found in the Trundle beds were figured by Gross (1971b, plate 7, figures 1,13,14), and captioned as lower jaw fragments of *Nostolepis striata*, based on the erroneous assumptions that (a) *Nostolepis* lower jaws had dentigerous bones, while the upper jaws had rows of tooth whorls, and (b) that the elements were from *Nostolepis*, whereas they are probably from *Poracanthodes* (this misconception is further elaborated in the next paragraph). Unfortunately, on most other ischnacanthid gnathals that have been described, any ossification of the cartilaginous jaw articulation areas is either not present or not preserved, and only rarely is the posterior end of the gnathal preserved intact. Reed (1986:415) proposed that some of the jawbones depicted by Ørvig (1957, plate 2, figures 1,2), which have an extra posterior "knob" could be from the upper jaw. However, there are no other features to distinguish them from 'proven' lower jaw bones. Certainly, on all three jaws figured by Ørvig with preserved posterior ends, the latter are splayed outwards. By comparison with these known cases, it seems possible (if only because of the lack of features attributable to known lower jaw gnathals) that the posterior jaw fragments described in the present paper are from the upper jaw. This interpretation is supported by a comparison with the articulated jaws of *Poracanthodes menneri* figured by Valiukevičius (1992, plate 11, figure 1). Although the posterior jaw bone segment is not preserved, the palatoquadrate cartilage retains the impression of the shape of this bone (see Figure 7A), and this compares well to the 'negative' of the 'positive' posterior jaw fragment (Figure 3A). Also, the impression left by the posterior end of the lower jaw bone in this specimen is consistent with that expected for the known lower jaw type.

Gross (1957, 1971b) described two jaw bone types from the Late Silurian Beyrichienkalk as *Nostolepis*- and *Gomphonchus*-type. The Trundle beds jaw

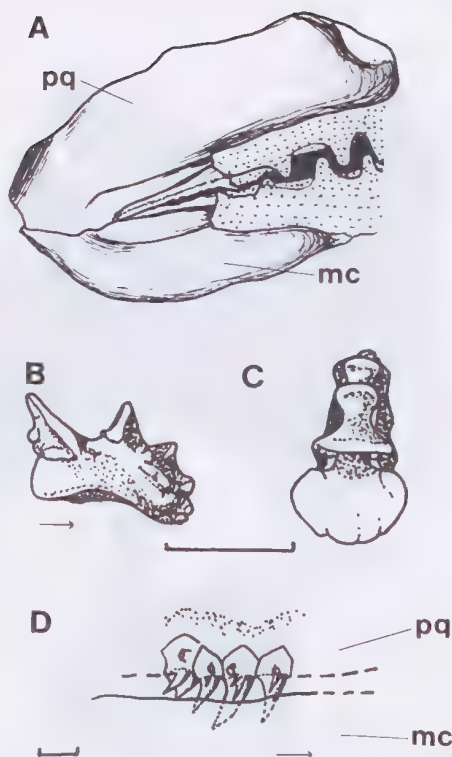


Figure 7 Articated jaws of *Poracanthodes menneri*, and climatid tooth whorls. A, *P. menneri* right upper and lower jaws, after Valiukevičius 1991, plate II, fig. 1: preserved dentigerous gnathals stippled; B, lateral view and C, anterior view, of tooth whorl of *Nostolepis striata*, after Gross 1957, taf. 4, fig. 7b,c; D, *Latviacanthus*, showing four tooth whorls, after Schultze and Zidek 1982, fig. 3. mc = Meckelian cartilage, pq = palatoquadrate cartilage. Scale bars = 1.0 mm; arrow indicates rostral direction.

fragments (Figure 3C–F) are very similar to examples that were attributed by Gross (1971b, figure 9A–F) to *Nostolepis*, but which have since been removed to *Gomphonchus* (Denison 1976). As well as having a medial tuberculated ridge, the jaw bone described here has a similar arrangement of side cusps, with about three cusps both anterior and posterior to the main cusp in each tooth group. As noted by Denison (1976), the differences between the two types of jawbones may indicate that the two scale-based species to which he tentatively assigned them, *G. sandelensis* and *G. hoppei*, may not be congeneric. Indeed, following the validation of *Poracanthodes* as a distinct taxon by Valiukevičius' (1992) description of articulated specimens of *P. menneri*, it now seems the *Nostolepis*-type jaw bone belongs to *Poracanthodes*

or to a closely related genus. This hypothesis is supported by the composition of residues from Late Silurian beds of Cornwallis Island, Arctic Canada (Sample Tc415[4+5], Tom Uyeno collection), in which the only acanthodian remains are large scales of *Poracanthodes* cf. *P. porosus* co-occurring with jaw fragments of *Nostolepis*-type *sensu* Gross (personal observation). The occurrence of this type of jaw bone in the samples from Trundle beds, which have no *Poracanthodes* scales, but which do have scales of "*Nostolepis*" *guangxiensis* (Wang), resembling those called *Gomphonchus* cf. *G. hoppei* by Vieth (1980), and scales of a new ischnacanthid (Burrow in press), suggest that *Poracanthodes* and one of these species are closely related.

Histological structure of the jaw bones is not readily of use in determining their affinities; Gross (1971b:27) recognized similar hard tissues in both *Gomphonchus* and "*Nostolepis*" tooth cusps, and wide variation in the development of vascular canals and denteons in "*Nostolepis*" jaw bones. Also Ørvig (1973:125) noted that the side cusps in both *Gomphonchus* and "*Nostolepis*" are formed of a similar dentinous tissue.

Jaw bone fragments similar to those described here have also been recorded from the Lower Devonian Obere Carazo Formation, Profil Arauz, of Palencia, Spain (figured as "*Ischnacanthidae* indet." by Mader 1986, plate 3, figures 15,17a-c).

Tooth whorls

By comparison with the lower jaw symphyseal tooth whorls of articulated ischnacanthids, the symmetrical tooth whorls (e.g., Figure 4A) were probably positioned in the lower jaw symphysis. These tooth whorls are similar to those attributed to *Gomphonchus sandelensis* (Gross 1967), but most of them differ in having more side cusps (up to eight per tooth row). Similar tooth whorls have also been described from the Lower Devonian Nakaoling Formation ("Siegenian") and Yukiang Formation (early Emsian) in the Liujing area of Hengxian County, China, assigned to *Gomphonchus liujingensis* Wang 1992, a species described on the basis of scales and a tooth whorl. The cusps of the paratype tooth whorl figured by Wang (plate 3, figure 2a-c), have a circular parabasal section rather than the sub-triangular section of the Trundle beds symmetrical tooth whorl MMMC02249 (Figure 4A), and are conspecific with scales that have a pore canal system in the crown. As mentioned above, the robustness, size, and relative size and number of tooth cusps in the Trundle beds specimens is quite variable. Histological structure of these tooth whorls (e.g., Figure 6C) appears identical to that of "*Gomphodus*" tooth whorls as illustrated by Gross (1957, plate 3, figures F-H). While some of the Trundle beds tooth

whorls have cusps with a sub-triangular parabasal section, others, which lack the distinctive ridges, have a circular parabasal section. The triangular shape of the bone base of the tooth whorls indicates they are ischnacanthid symphyseal whorls, as climatiid tooth whorls have parallel sides (e.g., Figure 7B,C). However, the variation in the Trundle beds tooth whorls indicates they could have derived from more than one ischnacanthid species.

The multiple tooth whorl (MMMC02250, Figure 4D,E) appears comparable to the spiky 'hedgehog'-like tooth whorls in the mouth cavity of *Gomphonchus* (Gross 1957, plate 3, figures 1,4-6). The tooth whorls described by Gross have strongly spiralled bases, but the Trundle beds tooth whorl is incomplete. In other features – three tooth rows, smooth recurved teeth and gradual increase in tooth size anterior to posterior – they are similar. In all ischnacanthid genera described from articulated specimens the symphyseal tooth whorl (where present) is positioned in the lower jaw. Several types of isolated jaw bones have been figured (e.g., "*Gomphodus*" in Gross 1957, and *Taemasacanthus* in Long 1986, fig. 4A,D) with a cusp-free anterior segment. Perhaps some genera had parasymphyseal tooth whorls/tooth whorl complexes on, but not ankylosed to, the jaw bone or cartilage in a comparable position to the tooth plates of dipnoans, or the tooth whorls of other higher osteichthyans (e.g., onychodontids). In its shape and robustness the asymmetrical tooth whorl described here certainly bears comparison with such tooth plates. These similarities support the possibility that the element had a parasymphyseal position; alternatively, it may have been a pharyngeal element.

Denticulated plates plus tooth whorl

These elements (Figures 4F, 6D,E) do not match any previously described dental elements. Mader (1986, plate 3, figure 6a,b) figured a tooth whorl from the Lower Devonian Obere Carazo Formation of Spain which appears morphologically intermediate between this tooth whorl type and the fragile 'Borstenplättchen' (i.e., bristle plates) which Gross (1971b) suggested may have been supported by the branchial arches. Mader made no suggestions regarding their original anatomical position. The asymmetry of the Trundle beds element type indicates that it was paired, and its worn tubercles suggest that it opposed another (possibly identical) dental element. It might originally have been positioned in the pharynx; however, if this element, and the multiple tooth whorl (MMMC02250) which has similar cusps, came from a different species to the rest of the described elements, there are other possibilities. The shape of the base, the denticles on the narrow

edges, and the wear on the denticulated surface, could indicate that it was supported by the jaw cartilage itself.

Perhaps these elements represent a dentition intermediate between the climatiid pattern of rows of tooth whorls, and the denticulated jaw bones of ischnacanthids. Nearly all climatiid tooth whorls described to date (e.g., from *Nostolepis striata* and *Climatius reticulatus*, Figure 7B,C) have flattened, blade-like cusps attached to a concave base of relatively constant width. *Latviacanthus* Schultze & Zidek 1982 is an exception: the cusps have a circular parabasal section, but unlike other climatiids the tooth whorl base concavity is at right angles to the curvature of cusps. That is, the cusps are directed rostro-caudally rather than medially, as in all other described species (Figure 7D).

Single teeth and tooth-like cones

The single teeth (Figure 5A) from the Trundle beds are similar to those previously attributed to *Gomphonchus* (Gross 1957). However, Gross' 'Dornzähne' have a broad concave base, whereas those from the Trundle beds do not. These teeth may be ontogenetically 'young' versions of the robust Type II dentition cones.

The two types of dentition cones, although bearing some similarity to phosphatized arthropod jaw fragments, appear identical to the cones described by Valiukevičius (1992), from the oral cavity of *Poracanthodes menneri*. The fragile Type I cones were possibly associated with the branchial arches. Although Valiukevičius (1992) suggested that the Type II cones were similarly positioned, their robustness could indicate a position further forward in the mouth cavity.

Many of the diverse acanthodian dental elements from the Trundle beds might derive from a single ischnacanthid species, but it is probable that they are from at least two species. As noted above, a large number of acanthodian scales has also been retrieved from the Trundle beds samples (Burrow in press); most of them have been assigned to "*Nostolepis*" *guangxiensis* Wang 1992 and a new species. The latter appears to belong to a group of acanthodians whose scales have a poracanthodid-type histology, but lack pore canal openings on the crown surface. Juozas Valiukevičius (Lithuanian Geology Institute, Vilnius) has also studied acanthodian scales from late Lochkovian deposits of the Baltic states, with this type of histology (pers. comm.).

A distinctive feature of all the tooth whorls and the jaw fragments is the arrangement of their cusps, with each large central cusp usually being flanked by two or three smaller cusps. Although the newly described element, the denticulated plate plus tooth whorl, and the multiple tooth whorl have a similar cusp arrangement to the other

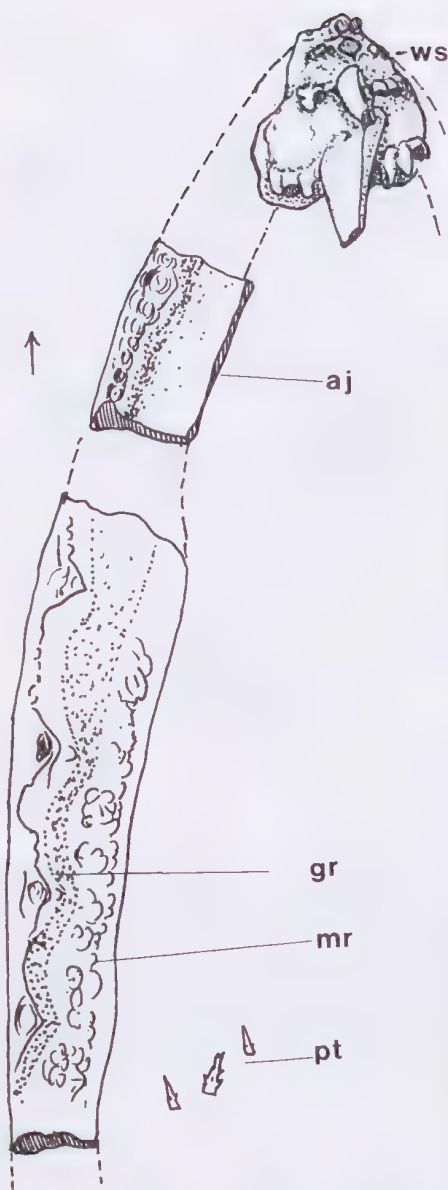


Figure 8 Hypothetical reconstruction of lower jaw of ischnacanthid from the Trundle beds, central New South Wales (individual elements not necessarily to scale). aj = anterior jaw bone fragment, gr = groove, mr = medial ridge, pt = palatine tooth, ws = symphyseal tooth whorl; arrow indicates rostral direction.

whorls and jaw fragments, the cusps of the former two have a circular parabasal section rather than the tri-carinate, or sub-triangular form of the cusps of the symphyseal tooth whorls and jaw fragments. In an attempt to reconstruct the original anatomical positions of the various dental elements, these two types are kept separate. The proposed lower jaw

reconstruction of the ischnacanthid fam., gen. et sp. indet. presented here (Figure 8), matches the pattern observed for *Poracanthodes menneri* Valiukevičius (1992). It incorporates all types of dental elements recorded for the latter species except the small pharyngeal tooth whorl. However, as neither of the Australian sciotaxa to which the elements probably belonged are classifiable as *Poracanthodes*, the jaw fragments and associated elements from the Trundle beds cannot yet be assigned with any certainty to either taxa.

CONCLUSIONS

The range of dental elements present in the Lower Devonian Trundle beds samples from New South Wales incorporates all known elements of ischnacanthid dentition, but also probable posterior ends of upper jaw gnathals, and at least one new form – the denticulated plate plus tooth whorls. The latter elements are of interest as they represent a dentition form which does not fit readily into recognized climatiid or ischnacanthid patterns. If the posterior ends of jaw bones do derive from the upper jaw, as proposed, they represent a previously unrecognized difference between ischnacanthid upper and lower jaw bones. The presence of those dental elements which can be certainly attributed to ischnacanthid acanthodians should prove of value in classifying the isolated scales present in the same samples.

ACKNOWLEDGEMENTS

I wish to thank Dr John Pickett and the Geological Survey of New South Wales for providing the samples; Dr Anne Kemp (University of Queensland) for use of stereo microscope and camera; Herr Jo Vergoossen (Groningen University, Netherlands) for critical evaluation and discussion; Rick Webb (University of Queensland) for SEM work on uncoated specimens; Dr Tony Thulborn (University of Queensland) and Dr Susan Turner (Queensland Museum) and an anonymous reviewer for comments on draft manuscripts. This is a contribution to IGCP Project 328: Palaeozoic Microvertebrates.

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Notes on the ethology of *Rolandia maculata* (Hymenoptera: Vespidae: Masarinae), a pollen wasp with a psammophore

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Abstract – *Rolandia maculata* (Meade-Waldo), a pollen wasp restricted to southwestern Australia, produces a single summer generation of adults. A nesting population was observed in Kings Park, Perth, where females excavated burrows solitarily in level sandy ground from late November to January. Females carried dry soil excavated from the burrows in a psammophore (formed by the posteriorly hollowed head capsule, propleura and fore legs, all of which bear fringes of long setae) and scattered it up to 4m from the burrow entrances.

The burrows and the brood cells constructed singly at the lower ends of burrows were uncemented and unlined. Provisions were typical of Masarinae in consisting of moist masses of pollen, the pollen being derived from flowers of *Jacksonia* species (Fabaceae). Nests were visited by the wasp *Hyptiogaster arenicola* Turner (Gasteruptiidae), an apparent parasitoid or cleptoparasite of the species.

INTRODUCTION

Masarinae are unusual among the aculeate wasps in having a strictly vegetarian diet in both larval and adult stages. Females provision their brood cells with pollen and nectar just as do the bees. However, our knowledge of the biology of Australian masarine wasps is very sketchy and observations are recorded for few species. *Rolandia* Richards, as interpreted by Snelling (1986), is an endemic Australian genus with four species¹. Hitherto, no detailed studies have been made of the habits of any *Rolandia* species and the limited published information has concerned floral preferences and nest locations (Richards 1968, Houston 1984, Snelling 1986). *Rolandia maculata* (Meade-Waldo) is endemic to southwestern Australia. Houston (1984) noted having examined a single incomplete nest burrow of this species in sandy soil but nothing else has been published regarding the ethology of the species.

The observations reported herein were made in a bushland area of Kings Park, Perth in the summers of 1992–93 and 1994–95, and at Neerabup National Park, ca. 34 km NNW of Perth, on 13 January 1995. In the first summer of observation, adult activity at Kings Park was noticed first on 17 November and return visits were made on 11 further occasions (24

and 27 November; 2, 3, 9, 10, 15 and 16 December; 6 January; and 12 and 22 February). Visits were made between the hours of 9 am – 5 pm (but chiefly between 10 am – 3 pm) and totalled in excess of 20 hours. All visits were made during warm to hot, sunny weather when adult activity could be expected.

OBSERVATIONS

Distribution and habitat

Perusal of literature records and specimen data labels in the insect collections of the Western Australian Museum (WAM) and the W.A. Department of Agriculture (WADA) reveals that *Rolandia maculata* has been collected only from coastal plain localities ranging from Moore River (110 km N of Perth) to Yallingup (ca. 200 km SSW of Perth). Its habitat consists of mixed woodland/heath communities, the upper storey of which is dominated by *Eucalyptus*, *Casuarina* and *Banksia*. The soils are predominantly sand derived from old coastal dune systems.

Nesting area

Nest burrows and females initiating burrows were distributed sparsely and apparently randomly along a 70 metre long section of a little used fire access trail in a bushland area of Kings Park (Figure 1). The surface of the trail was flat with white sand, bare for the most part but with a sparse cover of stunted grass and herbs (mostly dried off) and, in places, a sparse to dense covering

¹van der Vecht and Carpenter (1990) noted that *Rolandia* Richards, 1962, is a junior subjective synonym of *Metapargia* Meade-Waldo, 1911, and referred to J.M. Carpenter in an unpublished work as the authority of the synonymy. As Carpenter's work is still unpublished, I have preferred to retain use of the name *Rolandia*.



Figure 1 Trail in Kings Park used by nesting females of *Rolandia maculata*.



Figure 2 Female of *R. maculata* departing from her nest burrow, carrying a load of sand between her head and fore legs.

of fallen *Casuarina* 'needle' leaves. Despite searching, I could find no nest burrows nor nesting activity to the sides of the trail among the heath understorey nor along other trails in the general

vicinity. Excavation revealed that only the top few millimetres of the soil profile consisted of white sand. Beneath that, to a depth of about 18–20 cm, the soil was brown loamy sand laced with grass



Figure 3 Profile of head and forebody of *Rolandia maculata* female showing long setae comprising the psammophore (shorter, generally distributed setae omitted for simplicity). Scale line 1 mm.

and herb roots and deeper still was uniform yellow sand. The soil was damp throughout as a result of heavy rains preceding excavation.

Phenology

Comparatively few WAM and WADA specimens (other than those originating from this study) are labelled with their collection dates. Those with dates (both sexes) were collected in the months of December and January in various years.

On the first occasion I observed adults in Kings Park (17 November), both sexes were numerous at flowers of *Jacksonia* species and over the section of fire access trail described above. Many females were searching over the surface of the trail, some alighting intermittently to make exploratory excavations, while two other females were well advanced in excavating burrows. All specimens collected in November 1992 had entire wing margins indicating recent emergence (most specimens collected in December and January show slight to marked fraying of wing margins). Clearly, it was then early in the nesting season but probably activity had begun at least several days prior. A week of electrical storms with strong wind and heavy rain followed the first visit and must have caused a heavy mortality for, on my subsequent visit (24 November), only one male and one female were observed over the nesting site and only a few individuals were encountered each visit thereafter in December and January. No adults at all were observed during the February visits when the forage plants had few flowers remaining and it was evident that the nesting season had finished. In summary, the available evidence suggests that the flight season of *R. maculata* extends from mid November to mid January.

Nest architecture

Burrow entrances were simple holes in the sand, without any form of turret, reinforcement or closure. Several burrow entrances observed were partly concealed beneath some small object on the ground such as a sheoak fruit, a twig or fallen grass stalks, while two were quite exposed in bare sand. All burrows entered obliquely at about 30° below horizontal. Five nests were excavated. In each case, the burrows had been marked after *R. maculata* females were observed entering or leaving them. The oblique entrance galleries curved downwards sharply into vertical shafts which were horizontally displaced from the entrances by 2–3 cm (Figure 4). Entrance galleries and the shafts below them were 4–5 mm in diameter, round in section, unlined and uncemented. Freshly constructed brood cells were found in association with two shafts at depths of 28–32 cm, well into the yellow sand zone. No brood cells were found near the first shaft excavated which extended to a depth of only 10 cm and was plugged with white surface sand in its upper half. It appeared to have been abandoned while incomplete.

The second nest had one open cell at the lower end of the shaft. The cell was a 2 cm long lateral extension of the shaft and was not formed or lined in any detectable way. Resting on the floor of the cell at its inner end was a partially completed provision mass bearing a first instar larva and a flaccid egg chorion.

Three cells were located near the lower end of the third shaft (Figure 4). One, which was open and contiguous with the shaft, contained an elongate egg lying transversely across the inner end and a newly initiated provision mass. The other two cells were slightly deeper, closed and contained completed provision masses with feeding larvae. The cells radiated out in different directions and up to 3 cm from the shaft. Long axes of two cells were horizontal while that of the third was oriented 45° below horizontal.

The fourth and fifth nests excavated were marked while still open and occupied in early December and early January, respectively, but had been completed and deserted by their makers at excavation in February. Only the upper sections of the shafts which were filled with white surface sand could be traced but several cocoons were sieved from blocks of sand cut from 20–40 cm below the entrance of each nest. Two distinct kinds of cocoons were recovered. Three cocoons of one kind (presumed to be those of *R. maculata*) contained mature defaecated larvae while five others were old, vacated and sand-filled. Three of these vacated cocoons are believed to have been made by *Hyptiogaster* larvae (see Associated Organisms).

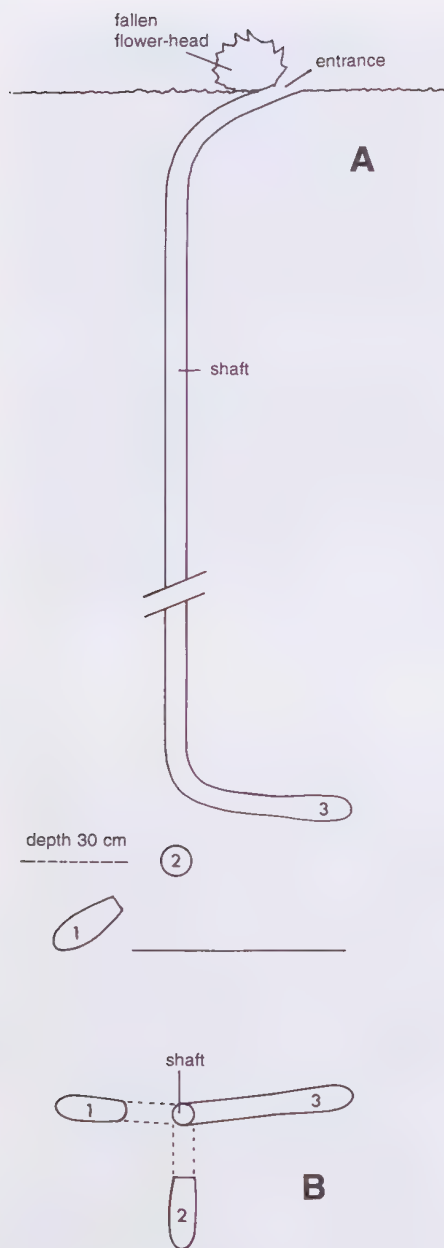


Figure 4 Details of a nest of *Rolandia maculata*: A, profile of partially completed nest; B, plan view of cells (1-3) showing relationship to shaft. Scale line 5 cm.

Cocoons

The occupied cocoons (Figure 5A) were spindle-shaped, light brown, 17-19 mm long, 5.5-6.0 mm in diameter and had sand grains adhering to their coarsely fibrous outer surfaces. Internally, they

were lined by a sparsely woven and very delicate layer of fine silk and between the outer and inner layers was a densely woven, felty layer of silk. Both outer and inner surfaces were quite dull. The cell mouth end of each cocoon had a vestibule separated from the main lumen by a partition, flat on the outer surface and concave on the inner. Faecal material formed a thin meconium covering the inner end of each cocoon.

Two larvae in cocoons were kept in an airconditioned laboratory and there was no indication of development when the larvae were inspected 12-14 months later. That the larvae were still alive was evident from writhing movements in response to touching.

Provisions

The provisions consisted of firm masses of moist orange pollen. Pollen samples taken from three provisions proved under microscopic examination to be homogeneous and consistent with being derived from *Jacksonia* species (Fabaceae), the observed forage plants. Completed provisions were rather "larviform" in appearance, being elongate, segmented and having 5-7 pairs of protuberances somewhat like caterpillar pseudopods on the underside. Masses were thickest towards the cell mouth and tapered towards the cell base. Evidently, the provision masses are formed of successive deposits of pollen, commencing in the inner ends of cells and progressing towards the cell mouth.

Female behaviour

Nest burrow construction

Females in the process of excavating burrows made frequent short flights from the entrance. For example, one female made nine flights during eight minutes of observation. Females always reversed out of their burrow entrances and hesitated for several seconds prior to taking flight. Typically, the flights were 3-5 seconds in duration, directly away from the burrow in a fixed direction to a set point 10-50 cm from the entrance and straight back again. However, one female repeatedly flew 4 m from her burrow. Females slowed as they approached their entrances but scuttled straight in after alighting. The purpose of these flights was not immediately apparent but proved to be for the purpose of disposing of excavated sand: a piece of blank card placed on the ground beneath the turnabout point of two females' flight paths revealed that the wasps dropped loose grains of sand there with every flight. Because the sand grains were scattered loosely, they spread imperceptibly over the surface and no tumulus was formed. Females carry the sand in a psammophore formed between the head,

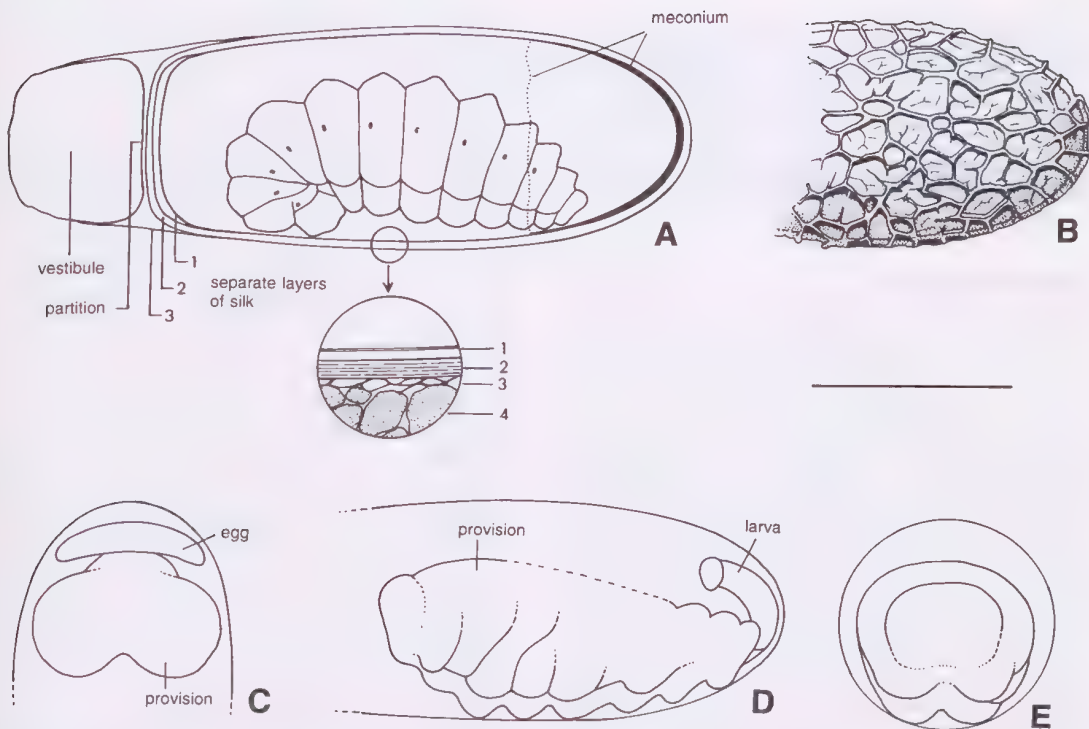


Figure 5 A, Cocoon of *Rolandia maculata* in longitudinal section showing dormant, post-defaecating larva, meconium (coating inner end of cocoon to dotted line) and (in circle) detail of cocoon wall (1, delicate inner layer of silk; 2, thick middle layer of silk; 3, network of coarse silk fibres attached to sand grains (4)); B, rear end of cocoon of *?Hyptiogaster arenicola* showing outer surface pattern; C, newly initiated provision mass of *R. maculata* with egg in inner end of cell (plan view); D, sketch of completed provision mass in brood cell (viewed from side and slightly from below) with newly hatched larva (some detail of upper surface of provision lost as a result of damage during excavation); E, same provision mass viewed from outer end. Scale line 5 mm.

propleura and fore legs (Figures 2, 3). The head capsule and the large mandibles are excavated posteriorly, forming a shallow basin with a distinct rim. A fringe of long, erect setae occurs along the rim. The propleuron is comparatively large and flat and also has lateral fringes of long, erect setae which mesh with those of the head forming a 'cage' which serves to contain sand grains at the sides. The fore legs have expanded fore femora, somewhat flattened on their anterior surfaces with a ventral fringe of long, erect setae, and support the loads of sand from below.

Foraging

Females were observed to forage only on yellow and red flowers of *Jacksonia* species. In Kings Park, the species visited were *J. sericea* Benth and *J. sternbergiana* Huegel. Both are leafless shrubs, the former having a dense spreading habit and not exceeding 60 cm in height, the latter having a spindly erect form and growing to 4 m. Most foraging adults were observed on *J. sericea*, females taking both nectar and pollen. Other *Jacksonia*

species at which *R. maculata* has been recorded include *J. stricta* Meissn. (Neerabup National Park) and *J. spinosa* (Labill.) (Moore River National Park).

Females spent 1–3 seconds on each flower and held their wings erect while alighted. When collecting both pollen and nectar, a female first probes deep into the nectary, then backs up slightly to hunch over the anthers (released from the flower's 'keel' by downward pressure from the wasps' mid and hind legs) and the anthers contact the underside of her thorax. The propleura, fore coxae, fore trochanters and mesepisternum are clothed with stiff erect setae, many of which are bent at the tips, and several pinned females in the WAM collection carry considerable amounts of pollen among these setae. Evidently, this vestiture serves as a pollen collector and the pollen is most likely groomed off to the mouth with the brush-like fore tarsi (although no direct observations were made to confirm this).

Male behaviour

Numerous males were observed flying

persistently within 30 cm of the ground over the nesting area at Kings Park in November and December. Occasionally, a male would alight on a plant stem and rest for a few seconds to a minute before moving on. Males were also observed patrolling flowers of *Jacksonia sericea*. However, no male/female encounters were observed at the nesting area or the forage plants.

Associated organisms

A gasteruptionid wasp, *Hyptiogaster arenicola* Turner, was the only organism found living in association with *R. maculata*. One to a few adults of *H. arenicola* were encountered at the nesting area on most visits from 27 November to 6 January. Females of this wasp were most often observed flying slowly over the nesting area just above the ground surface. They followed meandering paths and their manner suggested they were searching. When an *H. arenicola* female came close to an open burrow entrance of *R. maculata* it usually circled the entrance, all the while continuing to face it with antennae directed forward and downward. In most cases, after a brief inspection, the wasp would alight on a grass stem or some ground litter about 8–10 cm from the entrance, still facing it, and remain motionless. Occasionally, females shifted position but remained close to the burrows. On one occasion, a female *H. arenicola* was observed to enter a burrow. She had been perching close to the burrow entrance for four minutes when a *R. maculata* female arrived and entered the burrow. Eight minutes later (perhaps following the departure of the burrow occupant, although I did not observe this), the *H. arenicola* female began hovering again, moved to the burrow entrance, circled it once, alighted, turned 180° and reversed down the shaft. In less than 60 seconds, she reappeared, moved to a nearby stem where she groomed herself and then moved on.

One female of *H. arenicola* maintained a vigil near a burrow for many minutes but eventually moved on without entering it. The occupant of the burrow was not sighted during the wasp's vigil and I suspect that it is the departure of the host wasp from a burrow that stimulates the cleptoparasite to enter.

Further evidence that *H. arenicola* is cleptoparasitic in brood cells of *R. maculata* came in the form of three vacated cocoons found among occupied and vacated cocoons of the host. The cocoons were easily distinguishable from those of the host by being less fibrous and were partly composed of a hard blackish material (more so at the rear end) that had penetrated between grains of sand, forming a coarsely reticulate pattern on the outer surfaces of the cocoons (Figure 5B). Internally, the cocoons had a smooth, slightly shiny, translucent brown layer formed by a hard

amorphous material laid on a network of coarse brown silk fibres.

DISCUSSION

Gess and Gess (1992) provided a discussion of nesting in the subfamily Masarinae (*sensu* Carpenter 1982) and recognised seven basic nest types. Many masarine wasps construct cemented earth turrets and/or brood cells using either water or nectar as the bonding agent (nest types 1–6). One species, *Quartinia vagepunctata* Schulthess, nests in friable soil and constructs entrance turrets and brood cells of sand and silk (nest type 7). Nests of *Rolandia maculata*, being made in friable soil and having no cemented or bonded earth structures of any kind, fit none of the seven nest types and require an eighth category. In erecting the genus *Rolandia* (with *R. maculata* as the type and only known species), Richards (1962) remarked that "The very marked fringe of bristles on the periphery of the lower side of the head, around the oral fossa, is perhaps connected with the method of gathering food which would be well worth studying in life." However, Snelling (1986) noted the presence of such bristles in a few genera of Masarinae, including *Rolandia*, and termed them 'ammochaetae'. He speculated that they may form a psammophore, a "basket" for transporting sand particles excavated from nests. My observations have confirmed (at least for *R. maculata*) that Snelling's view is the correct one.

ACKNOWLEDGEMENTS

I am grateful to Mr R. Dixon and the Kings Park Board, Perth, for permission to undertake field studies in Kings Park. Mr John Jennings of the Waite Agricultural Research Institute, Adelaide, kindly identified specimens of *Hyptiogaster arenicola* and Drs Fred and Sarah Gess, Albany Museum, Grahamstown, South Africa, suggested some useful literature references.

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Manuscript received 28 April 1995; accepted 17 July 1995.

A new *Diplodactylus*, subgenus *Strophurus* (Lacertilia: Gekkonidae) from northern Australia

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Abstract – A new species of *Diplodactylus*, subgenus *Strophurus* is described from northern Australia.

INTRODUCTION

In 'Lizards of Western Australia part III, geckos and pygopods' (Storr *et al.* 1990: 31) we made special mention of an unusually large, pale *Diplodactylus mcmillani* collected 7 km SE of Mt Septimus [30 km E of Kununurra], Northern Territory. This is 250 km ESE of the nearest collecting site for *D. mcmillani*, which is in the Drysdale River National Park (15°03'S, 126°45'E). Recently, Mr N. Gambold, C.S.I.R.O. Tropical Ecosystems Research Centre, Division of Wildlife and Ecology, Darwin, Northern Territory, collected three specimens of a similar gecko from the Ord River basin. Their scalation is consistent with the pale specimen, but being recently collected they have a well preserved striped pattern which is similar, but different in detail, to other members of the *michaelseni* group, subgenus *Strophurus* (*sensu* Storr *et al.* 1990). These four specimens, all in the Western Australian Museum, are referred here to a new species.

SYSTEMATICS

Diplodactylus robinsoni sp. nov.

Holotype

R108646, ♂ collected by N. Gambold on 21 July 1991 at Mt Parker, Osmond Range, Western Australia, 17°10'S, 128°18'E.

Paratypes

Northern Territory: 7 km SE of Mt Septimus, ♂ (R67690).

Western Australia: Wade Creek, 17°11'S, 128°36'E (R108645), ♀, Mt Parker (R108647), ♂.

Diagnosis

Diplodactylus robinsoni is a large robust member of the *michaelseni* group, subgenus *Strophurus*, distinguishable from *D. taeniata* and *D. mcmillani* (other species in the *michaelseni* group in which the

rostral is precluded from the nostril by a prenasal) by its greater size (*D. robinsoni* 51–55 mm, mean 52.7; *D. mcmillani* 35–52 mm, mean 42.9; *D. taeniata* 32–44 mm, mean 38.6) and its colour pattern which is reduced to a series of simple wavy, web-like brown stripes, that is, it lacks the brown vertebral stripe of *D. taeniata* (Figure 1) and the white dorsolateral stripe of *D. mcmillani*.

Description

Snout-vent length males 51–55 (N3, mean 53), female 55.

Rostral hexagonal 2.0–2.5 times as wide as high (N4, mean 2.2), median groove extending down 30% of scale.

Rostral surrounded by first labial, prenasal (nearly as large as the first labial and broadly excluding rostral from nostril), 2 supraoculars and 3 or 4 (mostly 4) postnasals. Internasals 2 or 3 (mostly 2). Loreals 14–15 (N4, mean 14.5), upper labials 16–17 (N4, mean 16.5), 11–13 to immediately below eye (N4, mean 12.5). Undivided lamellae under fourth toe 5–6 (N4, mean 5.2).

Ventral scales slightly larger than dorsal scales. Males with 3 or 4 (mostly 3) spines on cloacal spur. No preanal pores.

Ground colour (except R67960 which is immaculate creamy-white consistent with lengthy exposure to light) drab brownish-grey, belly slightly paler. Top of head immaculate, temporals and nape sparsely flecked and spotted brown. Each flank with 6–8 brown, irregular, interrupted, spidery lines which are most regular and complete on lower flanks. Mid-dorsally spidery lines reduced to flecks and spots covering 1–5 scales. Limbs with brown flecks, belly with pale brown spots and flecks. No specimen has a original tail.

Distribution

Upper Keep and Middle Ord River drainages in north-west Northern Territory and east Kimberley, Western Australia respectively. See Figure 2.



Figure 1 Pattern differences between *Diplodactylus taeniata* (above) and *D. robinsoni*. Drawn from R70405 and R108645 respectively.

Remarks

Three other species in the *Diplodactylus michaelsoni* group, subgenus *Strophurus*, occur in the Kimberley region of Western Australia. *Diplodactylus jeanae* is only found in the southern Kimberley (Storr *et al.* 1990) and has the rostral in contact with the nostril. Of the remaining two species, *D. mcmillani* is considered a northwest Kimberley endemic and allopatric with *D. robinsoni*, leaving *D. taeniata* as the only species in the group sympatric with *D. robinsoni*.

Apart from size and pattern *D. taeniata* differs



Figure 2 Distribution of (O) *Diplodactylus mcmillani*, (●) *D. robinsoni* and (Δ) *D. taeniata* in the Kimberley, W.A.

from *D. robinsoni* in having fewer labials, fewer undivided lamellae and fewer cloacal spines (see Table 1). Furthermore, the rostral crease completely divides the rostral in *D. taeniata* but only partially divides the rostral in *D. robinsoni*.

D. robinsoni is most similar in body proportions and details of scalation to *D. mcmillani* and these taxa may be closely related. Apart from the differences in size and patterning noted earlier (see also Figure 1), *D. robinsoni* averages slightly higher numbers of subdigital lamellae and labials to below the eye (see Table 2).

All three Western Australian specimens were taken from *Triodia* on sandstone.

Etymology

This species is named after David Robinson in appreciation of his voluntary assistance to the Department of Herpetology, Western Australian Museum both in the field and in the laboratory.

Table 1 Comparison of size and numbers of cloacal spines, undivided subdigital lamellae and labials in *D. robinsoni*, *D. mcmillani* and *D. taeniata*.

		Size of males (SVL)	Size of females (SVL)	Overall size (SVL)	Cloacal spines (males)	Undivided lamellae	labials (to below eye)
<i>D. robinsoni</i>	N	3	1	4	4	4	4
	Range	51–55	55	51–55	3–4	5–6	11–13
	Mean	53.0		52.7	3.3	5.2	12.5
<i>D. mcmillani</i>	N	18	19	37	18	21	29
	Range	35–49	36–52	35–52	2–4	3–6	9–14
	Mean	41.7	45.9	42.9	3	4	11.2
<i>D. taeniata</i>	N	7	5	12	7	10	12
	Range	32–41	37–44	32–44	2–2	3–4	8–10
	Mean	37.4	40.2	38.6	2.0	3.6	9.0

ACKNOWLEDGEMENT

I am grateful to Lynne Broomhall of the Western Australian Museum for preparing Figure 1.

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- Storr, G.M., Smith, L.A. and Johnstone, R.E. (1990).
Lizards of Western Australia III, geckos and pygopods.
Western Australian Museum, Perth.

Manuscript received 12 April 1994; accepted 14 July 1995.

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Printed and published by the Western Australian Museum
© Western Australian Museum, June 1996
ISSN 0312 3162

Cover: Line drawing of *Liagoceradocus branchialis* sp.nov.

Biosystematics of Australian mygalomorph spiders: description of a new species of *Missulena* from southwestern Australia (Araneae: Mygalomorphae: Actinopodidae)

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Abstract – A new species of *Missulena* from west of Albany, southwestern Australia is described and notes on its biology presented. *Missulena rugosum* Ausserer is tentatively reinstated.

INTRODUCTION

The trapdoor spider genus *Missulena* Walckenaer, the only Australian representative of the Gondwanan family Actinopodidae, is widespread across the continent and occurs on some offshore islands but is absent from Tasmania. Early records of the genus in New Guinea (Rainbow 1920) are now generally discounted. The genus has long been recognised as taxonomically difficult. It was the first indigenous mygalomorph genus named from Australia. However, in spite of a revision of the genus by Womersley (1943) recognition of nominal species is in most cases difficult due to a combination of inadequate early nineteenth century descriptions, loss of many types, absence of locality data for early specimens and the conservative morphology. Perhaps the only named species which are unequivocally recognisable are *M. pruinosa* Levitt-Gregg from northern Australia, *M. bradleyi* Rainbow from mid-eastern Australia and two recently described species (Faulder 1995). Even the type species, *M. occatoria* Walckenaer as it is currently defined, appears to have several other species confused with it.

Main (1985) recognised seven species. Synonymy there of *M. rugosum* Ausserer with *M. occatoria* Walckenaer was perhaps in error and I now tentatively reinstate *M. rugosum*.

Regardless of the taxonomic confusion of the nominal species it is apparent from my field observations and an abundance of specimens (mainly males) in museums that there are many undescribed species. Richard Faulder is currently reviewing the genus and preparing redescrptions of those species recognised by him.

This paper provides a description of a new species from west of Albany, south western Australia. Female specimens from the Albany coastal region cannot unequivocally be associated with the male specimens on which establishment of the new species is based because another species with distinctive males (having red chelicerae)

occurs also in the same area.

Abbreviations: BYM, Barbara York Main collection (housed in the Zoology Department, University of Western Australia); WAM, Western Australian Museum.

SYSTEMATICS

Missulena torbayensis sp. nov.

Figures 1, 2; Table 1

Material examined

Holotype

♂, Rutherwood Road/South Coast Highway (Highway 1), Torbay, Nature Reserve, Western Australia, Australia, 16 June 1983, B.Y. Main, alive in pitfall trap (BYM 1983/140; WAM 1995/2).

Paratypes

Australia: Western Australia: All collected from pitfall traps. 1♂, data as for holotype, 20 June 1983–3 July 1983, (BYM 1983/143; WAM 1995/4); 1♂, West Cape Howe National Park, near granite dome above Dingo Beach, B.Y. Main, 4–26 August 1984 (BYM 1984/82); 1♂, West Cape Howe National Park, heath at eastern edge Lake William, B.Y. Main, 25 May 1985–13 June 1985 (BYM 1985/83; WAM 1995/3); 1♂, West Cape Howe National Park, karri/peppermint grove southwest of Lake William, B.Y. Main, 16 April 1987–12 May 1987 (BYM 1987/12).

Other Material

Australia: Western Australia: 1♂, Manjimup, 34°155'S, 116°09'E, 19 May 1976, J.D. Majer, pitfall trap (WAM 93/1698) (tentative identification); 1♂, Shannon River at Nelson Road 34°43'S, 116°21'E, M.S. Harvey and M.E. Bosfelds, 16–18 February 1990 (WAM 92/293) (tentative identification).

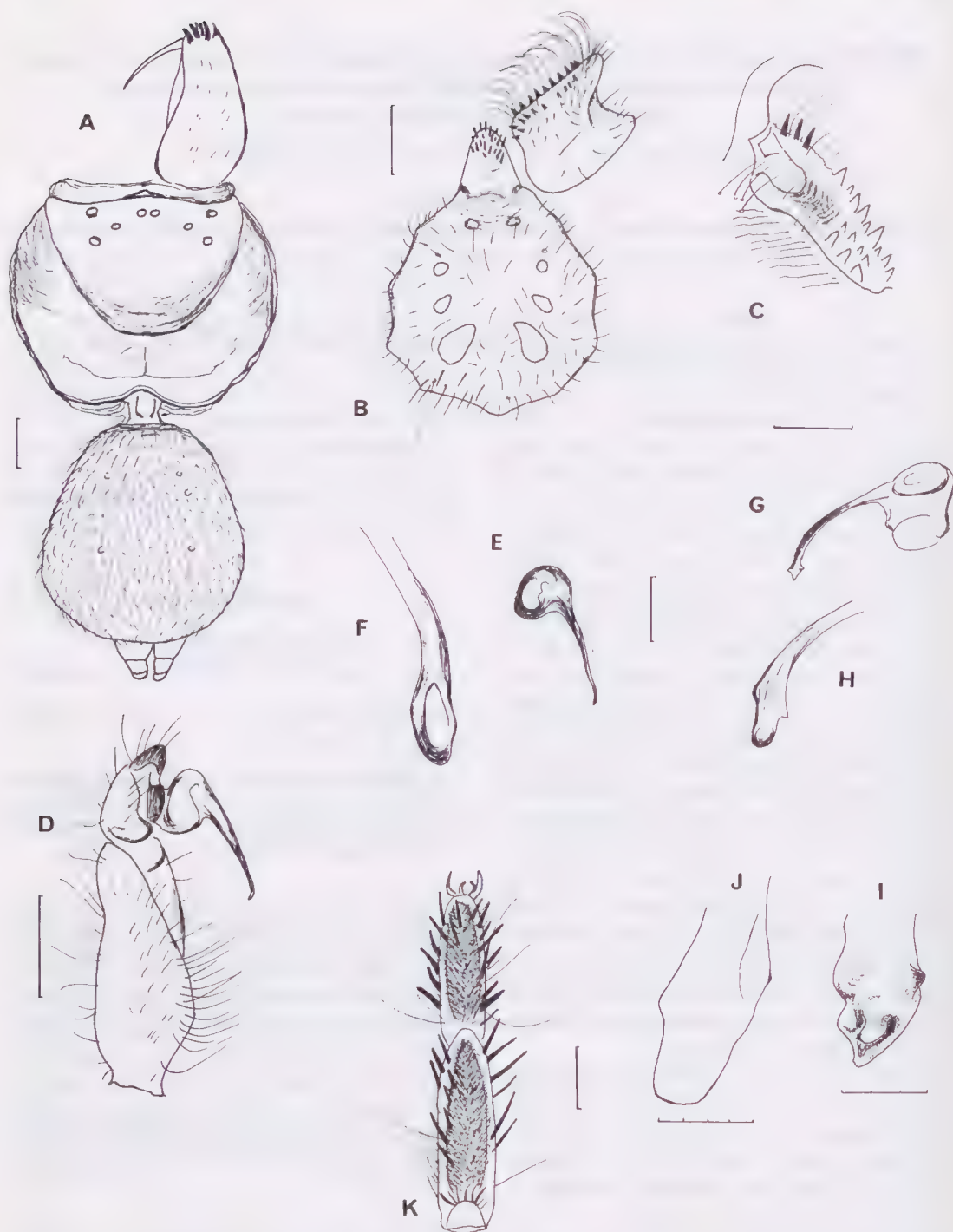


Figure 1 *Missulena torbayensis* sp. nov., male specimens. A-H, K, holotype; I, J, paratypes (BYM 1985/83 and BYM 1983/143). A, dorsal view carapace and abdomen; B, sternum, labium and left maxilla; C, right cheliceral groove; D, left palp, tarsus and tibia, proventral view; E, F, left bulb and embolus tip ventral; G, H, left bulb and embolus tip dorsal; I, J, left embolus tips; I, dorsal (see Fig. 2 B); J, ventral (see Fig. 2D); K, tarsus and metatarsus right leg IV ventral. Scale bars: A, B, D = 1.0 mm; E, G, K = 0.5 mm; I, J = 10 µm; C, F, H not to scale.

Diagnosis

Male spiders small and black with no white “patches” on abdomen; carapace length up to 4.0 mm. Carapace finely rugulose, caput with heavy rugosities. Teeth on inner row of cheliceral groove numerous (7–10) of uneven size, few (3) evenly sized relatively large teeth on outer and 3–4 smaller teeth on inner row. Differs from other small black species (*M. dipsaca* Faulder and *M. rutraspina* Faulder) by having “rasps” on all patellae instead of on patellae III only and by the “extra” pair of faint sigilla in the labial groove; from *M. rutraspina* by the rounded embolus tip and more numerous teeth in cheliceral groove rows and many long, pointed rastellum teeth; from *M. dipsaca* by presence of thin scopula on tarsus I and well developed scopula on tarsi III and IV (see Faulder 1995).

Description

Male (holotype)

Colour, body and legs uniformly black. Carapace finely rugulose, caput with heavy rugosities. Carapace length 4.0, width 5.1; caput width 3.9. Eyes, anterior width of group 2.8, posterior width 2.6; AME apart 0.1, ALE from AME 1.0, PLE from PME 0.5, ALE from PLE 0.3. Sternum and labium length 3.9, labium 1.3, sternum width 2.8. A pair of faint sigilla in labial groove and three discrete pairs

with posterior pair the largest and pear shaped. Labium with about 20 pin-like cuspsules in apical third. Maxillae with dense line of pin-like cuspsules on anterior margin extending onto rest of maxillary lobe. Chelicerae heavily rugulose, with transverse ridges on outer faces. Rastellum, about eight long pointed teeth on low mound. Groove with large teeth on both margins; (right) 9 unevenly sized prolateral (inner), 3 evenly sized retrolateral (outer) and 4 smaller teeth in intermediate row; (left) 10, 3, 4 respectively. Legs. Spination of legs I and IV. I, tarsus rv 4, v 3, pv 3; metatarsus rv 3, v 5, pv 7, tibia rv 4, v 6, pv 1 large apical spine. Prolateral rasp (or “rastellum”) on all patellae, very dense (at least 30 spines) on patella I, less dense (about 8) on II, very dense (at least 30) on III, less dense (about 25 short spines) on IV. Scopulae. I, a few sparse hairs on tarsus, II, absent, III and IV well developed scopula on tarsus and metatarsus. Tarsal claws. Teeth on paired and median claws. Right side. I, P 5, R 3 (distal tooth bicuspid), median 2. II, P 5, R 5, median 3. III, P 4, R 4?, median 2. IV, P 5, R 3, median 1. Genital area with about 40 pronounced fusules. Palp bulb typical of the genus, that is with a long tapering embolus. Embolus tip viewed ventrally, spoon shaped and rounded in outline; dorsally with small lateral processes (Figures 1 G–J and 2 A–D).



Figure 2 *Missulena torbayensis* sp. nov. bulb and embolus of paratypes. A, B, dorsal (BYM 1985/83) see Fig. 1 I; C, D, ventral (BYM 1983/143) see Fig. 1 J. Scale bars: A, C = 1.0 mm; B, D = 10 µm.

Table 1 *Missulena torbayensis* sp. nov., leg dimensions, holotype male. Tibial index = 100 X width of patella/length of tibia +patella (Petrunkevitch 1942).
Leg formula (length of leg divided by length of carapace):
1/2.7, 4/2.62, 2/2.25, 3/2.15

	F	P	Ti	Mt	T	Total
I	3.3	1.8	2.3	2.2	1.2	10.8
II	2.8	1.4	1.8	1.8	1.2	9.0
III	2.6	1.8	1.2	1.8	1.2	8.6
IV	3.2	1.9	2.0	2.1	1.3	10.5
Palp	2.8	1.6	2.4	—	1.0	7.8

Width of patella I at knee = 0.4; tibial index = 19.51
Width of patella IV at knee = 0.8; tibial index = 20.51

Variation

There is some variation in body size and all meristic characters such as leg spination, maxillary and labial spinules and teeth on groove of cheliceral fang. Variation of carapace length/width and numbers of teeth on inner, median and outer rows of right/left cheliceral groove of specimens additional to holotype from Torbay/West Cape Howe: 3.4/4.1; 8, 3+1minute, 3/7+several minute, 3.7-3 (BYM 85/83); 3.5/4.4; — (BYM 83/143); 3.5/4.6; 8, 4, 3/9,3,3 (BYM 84/82); 3.8/4.8; 9, 3, 3/7, 3, 4 (BYM 87/12).

BIOLOGY

Habitat

All the Torbay and West Cape Howe sites from where the spiders were collected are damp, shaded situations, although the ground may be dry on the surface during summer. The Rutherford Road reserve is a mixed jarrah/redgum woodland with shrubby, close undergrowth. The pitfall traps were sited along a permanently shaded drainage course which although lacking defined banks is wet in the winter with some surface water. The granite knob above Dingo Beach provides runoff into a scrubby paperbark swamp. The Lake William heath site is along a gentle slope down to a creek which runs vigorously in the winter and its broad, flat bed is wet enough to provide habitat mounds for pitcher plants (*Cephalotus follicularis*). The other West Cape Howe site is a small karri forest grove in a gully which drains into the southwest side of Lake William. It is likewise permanently damp and the heavily littered ground is deeply shaded with a thicket of acacias, reeds and other shrubs.

Phenology

All the Torbay/West Cape Howe specimens were collected during late autumn/winter from pit traps which were permanently open for at least 18 months. Similarly the Manjimup specimen was

collected in a pitfall trap during winter. Hence it is deduced that like most other species of *Missulena* the species mates during the autumn/winter. The Shannon River specimen, although collected in February was described as entangled in an amaurobiid web. As the specimen was dead and dry it may have been in the web for several months (M.S. Harvey, pers. comm.)

The lack of red or blue colouring of males of this species is of interest in relation to the habitat, that is, dark "closed canopy" situations. It is presumed that males, like most other species, wander during the daytime. It is probable that the bright colours of open habitat species are a defence against vertebrate predators and I postulate that such colouration mimics offensive insects such as mutillid wasps, although no specific models have been identified. Coyle and Shear (1981) suggested that the diurnally wandering males of *Sphodros* species, which are similarly brightly coloured may "have evolved a defensive mechanism of generalized wasp-ant mimicry in response to selection pressure from visual vertebrate predators". Possibly the species of *Missulena* with entirely black males such as that of the species described here, are confined to habitats with low, dense vegetation where disruptive or warning colours would have no significance.

ACKNOWLEDGEMENTS

I thank M.S. Harvey for making available *Missulena* specimens in the Western Australian Museum collection. I am grateful for a permit from the Department of Conservation and Land Management to collect spiders in parks and reserves. I thank Tom Stewart for preparing the scanning electron micrographs. Helpful comments from two referees were greatly appreciated.

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Manuscript received 23 January 1995; accepted 28 June 1995.

A review of the water mite family Pionidae in Australia (Acarina: Hygrobatoidae)

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Abstract – The Australian Pionidae consists of 11 species in six genera: *Larri* gen. nov. (with type species *L. laffa* sp. nov.), *Australotiphys* Cook (with *A. magnisetus* Cook, *A. himonius* sp. nov. and *A. barmutai* sp. nov.), *Acercella* Lundblad (with *A. falcipes* Lundblad and *A. poorginup* sp. nov.), *Piona* Koch (with *P. cumberlandensis* (Rainbow), *P. australica* K.O. Viets, *P. puripalpis* K.O. Viets, *P. murleyi* sp. nov. and *P. marchanti* sp. nov.). Mating in *Acercella falcipes* Lundblad and *Piona cumberlandensis* (Rainbow) is briefly discussed.

INTRODUCTION

Water mites of the family Pionidae are widespread throughout the Holarctic region where many genera are currently recognised (Cook 1974; Smith 1976; Simmons and Smith 1984). The fauna of the southern hemisphere is less well known and only diverse genera such as *Piona* Koch have been recorded frequently. Nevertheless, a distinct and very interesting Australian pionid fauna is present.

The first described Australian species, *Atax cumberlandensis* Rainbow, was not recognised as a member of the genus *Piona* until 1986 (Cook 1986). *Piona uncatiformis* and *Acercella falcipes* were described by Lundblad (1941), and two further species of *Piona* were added by K.O. Viets (1980, 1984). The enigmatic *Australotiphys magnisetus* Cook was described by Cook (1986). With the recent discovery of additional species of these three genera, as well as an undescribed genus from southwestern Australia, it became apparent that a review of the Pionidae of Australia would be profitable. The results of that study are presented here.

MATERIALS AND METHODS

Specimens are lodged in the following repositories:

- ANIC Australian National Insect Collection, Canberra
- AM Australian Museum, Sydney
- CNC Canadian National Collection, Ottawa
- DCC D. R. Cook collection, Detroit
- NMV Museum of Victoria, Melbourne
- QVM Queen Victoria Museum, Launceston
- SAM South Australian Museum, Adelaide
- SMNH Swedish Museum of Natural History, Stockholm

- TM Tasmanian Museum and Art Gallery, Hobart
- VC Viets private collection, Wilhelmshaven
- WAM Western Australian Museum, Perth

Methods follow Harvey (1987). Where the measurements are expressed as a fraction, the numerator refers to the length of the structure and the denominator refers to its width. Abbreviations for glandularia follow Harvey (1987): dg1–5 refers to the dorsoglandularia series, lg1–4 refers to the lateroglandularia series, and vg1–5 and vgx refers to the ventroglandularia series. Unless otherwise stated, the body colour is of specimens fixed and stored in Koenike's solution (Cook 1974), and refers to the sclerotized portions of the body (e.g., legs, coxae), rather than the soft portions. Those specimens denoted as 'SL' are mounted on slides, while those denoted as 'FL' are retained in fluid.

The terminology of water mite pedipalp and leg segments has been inconsistently applied by various workers. I here propose to alter the system that I have previously employed to name the leg segments, and replace them with names used in other arachnid groups (e.g. Shultz 1989, 1990; Harvey 1992), thus providing consistency within the class. Nearly all arachnids have six segments in the pedipalp (coxa, trochanter, femur, patella, tibia and tarsus), and seven segments in the legs (coxa, trochanter, femur, patella, tibia, metatarsus and tarsus) which clearly points to the homologous nature of leg segmentation within the Arachnida.

SYSTEMATICS

Family Pionidae Thor

Remarks

Recent diagnoses and classifications of the Pionidae (Cook 1974; Smith 1976) have emphasised

the lack of definite apomorphies, even when the critically important larvae are taken into consideration. One of the most perplexing taxa is *Wettina* Piersig which was considered to be the sister-group of the remaining pionids by Smith (1976). I believe a case could be made for the removal of *Wettina* from the Pionidae and placing it closer to the aturid subfamily Frontipodopsinae (Harvey 1990). Even with *Wettina* removed, the remaining group of genera lacks autapomorphies and the task of delimiting the Pionidae remains a severe difficulty (Cook 1974, in particular the key on p. 26).

Key to Australian species of Pionidae

Males

1. No segments of leg IV modified (Figures 8, 20, 30); tarsal claws of leg III of similar size and shape 2
At least one segment of leg IV modified (e.g. Figures 40, 62–64); tarsal claws of leg III of different sizes and shape (e.g. Figures 39, 61) 5
2. Three pairs of acetabula (Figure 5) *Larri laffa* sp. nov.
More than three pairs of acetabula (Figures 12, 15, 25) *Australotiphys* 3
3. Setae of tibia and metatarsus IV thickened (Figure 20); ventral shield present (Figures 12, 14) 4
Setae of tibia and metatarsus IV not thickened (Figure 30); ventral shield absent, although with 2 pairs of lateral setae (Figure 24) *Australotiphys barmutai* sp. nov.
4. Glandularia lg1 and vg3 situated on ventral shield (Figure 14) *Australotiphys himonius* sp. nov.
Glandularia lg1 and vg3 situated on dorsum (Figure 11) *Australotiphys magnisetus* Cook
5. Metatarsus IV with dorsal blade-like expansion (Figures 40, 50); tibia of leg IV without dorsal concavity containing several stout peg-like setae (Figures 40, 50) *Acercella* 6
Metatarsus IV not modified (e.g. Figure 62); tibia of leg IV with dorsal concavity containing several stout peg-like setae (e.g. Figures 62–64) *Piona* 7
6. Dorsal blade like-expansion of metatarsus IV very thick (Figure 40) *Acercella falcipes* Lundblad
Dorsal blade-like expansion of metatarsus IV very thin (Figure 50) *Acercella poarginup* sp. nov.

7. Genital field with deep central pit *Piona cumberlandensis* (Rainbow)
Genital field without central pit (Figures 56, 68, 80) 8
8. Pedipalpal tibia slender, lacking distinct ventral setiferous tubercles (Figure 99) *Piona puripalpis* K.O. Viets
Pedipalpal tibia moderately stout, with distinct ventral setiferous tubercles (Figures 65, 76, 88) 9
9. Pedipalpal tibia with distal thickened seta (Figures 65, 76); all acetabula incorporated into acetabular plate (Figures 56, 68) 10
Pedipalpal tibia with sub-distal thickened seta (Figure 88); only some acetabula incorporated into acetabular plate (Figure 80) *Piona murleyi* sp. nov.
10. Anterior claw of leg III without ventral clawlet (Figure 61) *Piona australica* K.O. Viets
Anterior claw of leg III with ventral clawlet (Figure 72) *Piona marchanti* sp. nov.

Females¹

1. Three pairs of acetabula (Figures 6, 37, 47) 2
More than three pairs of acetabula (Figures 18, 28, 57, 70, 82, 94) 4
2. Excretory pore surrounded by sclerotized ring (Figures 35, 45) *Acercella* 3
Excretory pore not surrounded by sclerotized ring (Figure 3) *Larri laffa* sp. nov.
3. Pedipalpal tibia with 2 large ventral setiferous tubercles *Acercella poarginup* sp. nov.
Pedipalpal tibia with 2 small ventral setiferous tubercles *Acercella falcipes* Lundblad
4. Coxae fused in mid-line (Figures 17, 27); dorsalia and glandularia platelets large (Figures 16, 26) *Australotiphys* 5
Coxae not fused in mid-line (Figures 59, 69, 81, 93); dorsalia and glandularia platelets small (Figures 58, 92) *Piona* 6
5. Ventral shield present (Figure 14) *Australotiphys himonius* sp. nov.
Ventral shield absent, although with 2 pairs of lateral setae (Figure 27) *Australotiphys barmutai* sp. nov.
6. Pedipalpal tibia slender, lacking distinct ventral setiferous tubercles (Figure 100) *Piona puripalpis* K.O. Viets

¹ Those of *Australotiphys magnisetus* Cook not known

- Pedipalpal tibia moderately stout, with distinct ventral setiferous tubercles (Figures 66, 77, 89) 7
7. Acetabula arranged in 2 distinct, circular groups *Piona cumberlandensis* (Rainbow)
- Acetabula arranged in 2 semi-circular rows (Figures 57, 70, 82) 8
8. Dorsal setae of pedipalpal femur and patella simple (Figures 66, 77).... *Piona australica* K.O. Viets, *Piona marchanti* sp. nov.
- Dorsal setae of pedipalpal femur and patella setose (Figure 89)..... *Piona murleyi* sp. nov.

Subfamily Huitfeldtiinae K. Viets

Larri gen. nov.

Type species

Larri laffa sp. nov.

Diagnosis

Legs III and IV of male unmodified. Body without accessory sclerotization. Genital field with 3 pairs of acetabula. Excretory pore not surrounded by sclerotized ring.

Description

Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and 6 pairs of ventroglandularia. Venter: coxae not fused into single plate; excretory pore not surrounded by sclerotized ring. Genital region: 3 pairs of circular acetabula; ♂ acetabular plate with medial seta in addition to normal setae, and flanked by several setae. Pedipalpal tibia with 2 ventral setae situated in small tubercles. Legs: unmodified; swimming setae present on all legs.

Remarks

This genus is one of the most plesiomorphic pionid genera, and appears to most closely resemble the Holarctic genus *Huitfeldtia* Thor, from which it differs by the presence of only three pairs of acetabula.

Etymology

The generic epithet is an arbitrary combination of letters, and is feminine in gender.

Larri laffa sp. nov.

Figures 1–10

Material Examined

Holotype

♂, Poorginup Swamp, Western Australia,

Australia, 34°33'S, 116°44'E, 4 September 1985, M.S. Harvey, T.J. Doeg (WAM 88/2929; SL).

Paratypes

Australia: Western Australia: 2♂, 3♀, 1 deutonymph, same data as holotype (WAM 88/2930–2933, 2939–2940; SL, FL); 2♂, 2♀, same data as holotype (NMV K857–858, K995–996; SL, FL); 1♂, 1♀, same data as holotype (CNC; SL); 1♂, 1♀, same data as holotype (DCC; SL); 2♂, 3♀, Lake William, West Cape Howe Natl Park, 35°05'S, 117°36'E, 3 September 1987, M.S. Harvey, J.D. Blyth (WAM 88/2934–2938; SL); 2♂, 3♀, same data (NMV K861–863, K997–998; SL, FL); 2♂, roadside pool, Chesapeake Road near crossing of Gardiner River, 34°48'S, 116°10'E, 29 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/2941–2942; FL).

Diagnosis

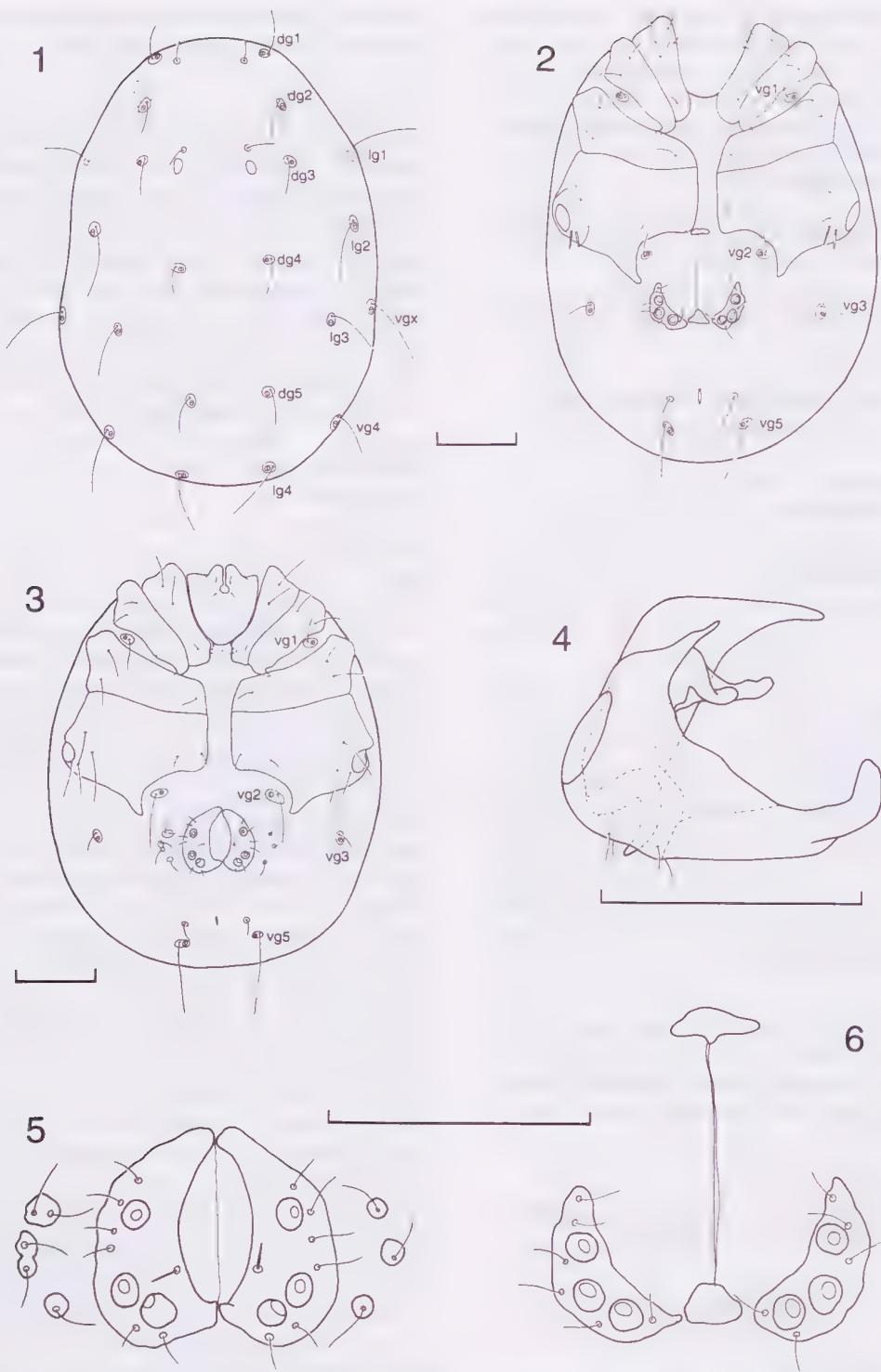
As for genus.

Description

Adult

Colour pale purple. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and 6 pairs of ventroglandularia (Figures 1–3). Dorsum (Figure 1): with 1 pair of dorsalia slightly posterior to postocularia. Venter (Figures 2–3): coxae not fused into single plate; apodemes of coxa I short; coxae I not fused in mid-line; suture lines between coxae III and IV reaching mid-line, extending laterally; excretory pore not surrounded by sclerotized ring. Genital region (Figures 5–6): 3 pairs of circular acetabula; 5–6 (♂), 5–8 (♀) pairs of small setae present on lateral margin of acetabular plates, a further medial seta present in ♂; acetabular plate of ♂ flanked by several setae. Chelicera stout (Figure 4). Pedipalp (Figure 9): tibia with 2 ventral setae situated in small tubercles, and a single distal, medial seta. Legs (Figures 7–8): unmodified; with swimming setae arranged as follows: leg I: ♂, tibia 0–2, ♀, tibia 1–3, metatarsus 0–2; leg II: ♂, patella 1, tibia 4, metatarsus 4–5, ♀, patella 1, tibia 5–6, metatarsus 3–5; leg III: ♂, patella 1, tibia 4–5, metatarsus 5–6, ♀, patella 1, tibia 6, metatarsus 6–7; leg IV: ♂, patella 1, tibia 4–5, metatarsus 5–7, ♀, patella 1, tibia 4–5, metatarsus 5–7; male legs III and IV not modified.

Dimensions (µm), ♂ (♀): body 531–570/384–429 (506–864/408–518); capitulum length 100–107 (96–121); chelicera length 129 (121); genital field 67–89/84–93 (111–182/108–160). Pedipalp: trochanter 25–29 (25–30), femur 80–84 (86–95), patella 45–52 (48–57), tibia 84–91 (85–99), tarsus 50–51 (49–60). Leg I: trochanter 54–57 (57–65), femur 58–69 (66–80), patella 87–95 (91–102), tibia 115–129 (127–148), metatarsus 135–148 (147–166), tarsus 158–180 (141–186). Leg IV: trochanter 87–99 (94–102), femur 78–



Figures 1-6 *Larri laffa* sp. nov.: 1, dorsal aspect, paratype ♀; 2, ventral aspect, paratype ♀; 3, ventral aspect, holotype ♂; 4, capitulum, lateral aspect, paratype ♀; 5, genital field, holotype ♂; 6, genital field, paratype ♀. Scale lines = 100 µm.

86 (83–102), patella 108–113 (115–140), tibia 137–151 (148–179), metatarsus 157–180 (164–200), tarsus 141–173 (142–192).

Deutonymph

Much as in adults except that vgx is absent; genital region with 2 pairs of acetabula.

Dimensions (µm): body 464/365.

Remarks

This lotic species has been collected from only three localities in southwestern Australia (Figure 10).

Etymology

The specific epithet is an arbitrary combination of letters.

Australotiphys Cook

Australotiphys Cook, 1986: 202.

Type species

Australotiphys magnisetus Cook, 1986, by original designation.

Diagnosis

Legs III and IV of male unmodified, except for the presence of enlarged setae on leg IV in two species. Body with accessory sclerotization. Genital field with many pairs of acetabula. Excretory pore surrounded by sclerotized ring.

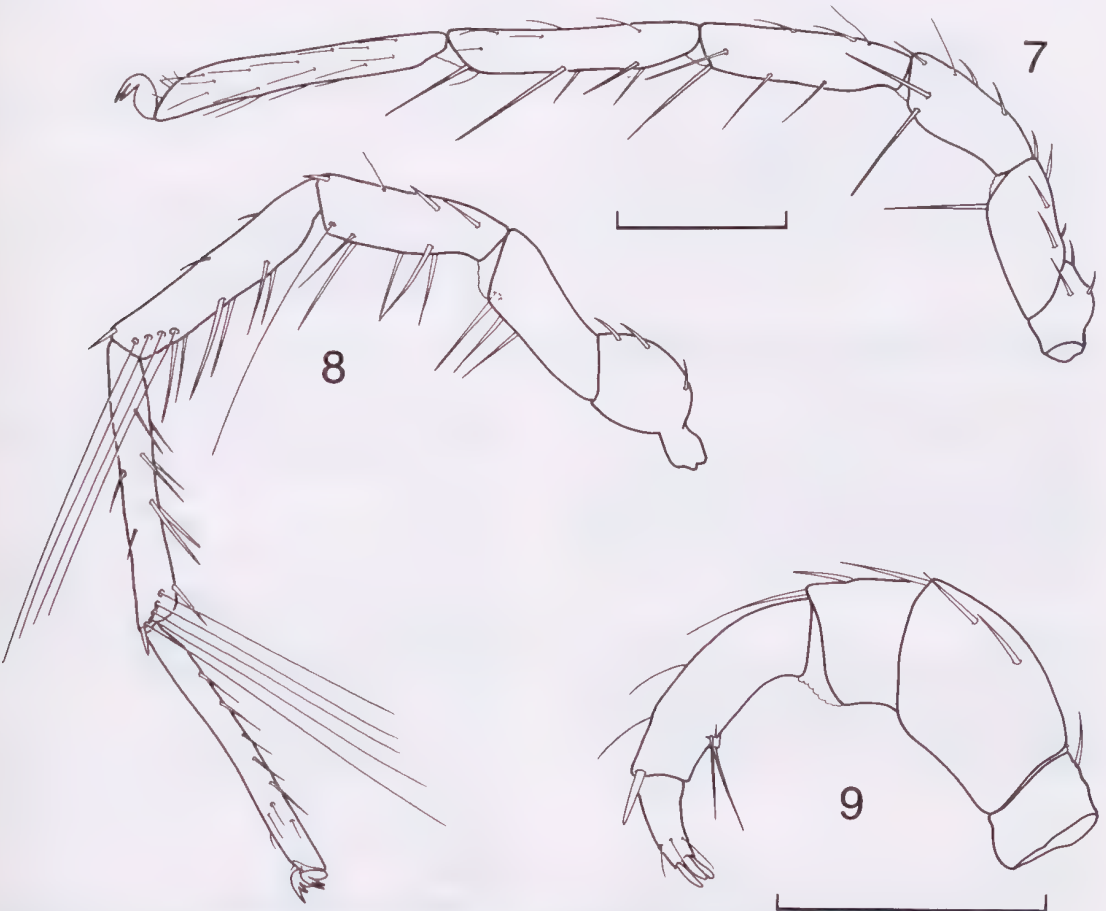
Remarks

This genus was erected by Cook (1986) for an unusual species from New South Wales known only from a single male. Two additional species have recently been collected and are described below. The genus has a wide, apparently disjunct distribution in Australia, with separate species known from northeastern New South Wales (*A. magnisetus*), northern Australia (*A. himonius*) and southwestern Australia (*A. barmutai*) (Figure 10).

Australotiphys magnisetus Cook

Figures 10–12

Australotiphys magnisetus Cook, 1986: 202, figs 1059–1060, 1062–1068.



Figures 7–9 *Larri laffa* sp. nov., holotype ♂: 7, left leg I; 8, left leg IV; 9, right pedipalp. Scale lines = 100 µm.



Figure 10 Map of Australia showing known distributions of *Larri* and *Australotiphys* spp.

Material Examined

Holotype

♂, Collins Creek at Collins Creek Road, 4 km N. of Wangaree, New South Wales, Australia [28°29'S, 152°58'E], 21 April 1981, D.R. Cook (NMV K580; SL).

Diagnosis

Tibia and metatarsus of male leg IV with thickened setae. Male with ventral shield extending from coxae; glandularia lg1 and vg3 not situated in ventral shield; glandularia vgx situated in ventral shield.

Description

Adult Male

See Cook (1986). Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and

6 pairs of ventroglandularia; lg1 and vg3 situated on dorsum (Figures 11–12).

Remarks

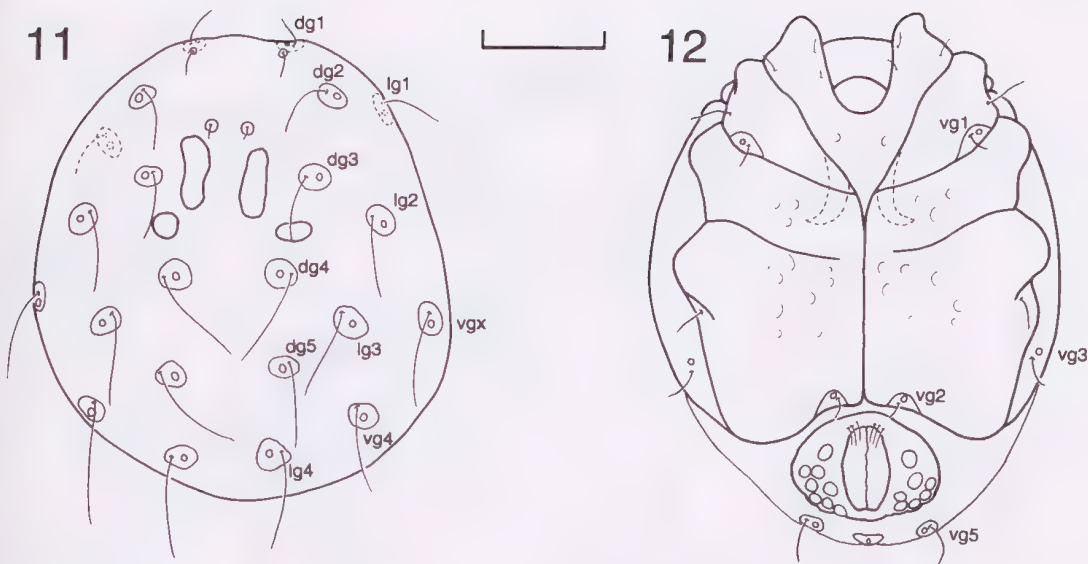
This species is only known from the holotype male, and differs from *A. himonius* by the positions of lg1 and vg3. The description by Cook (1986) of the holotype is complete and need not be repeated here, but figures are presented to allow for identification of the glandularia.

Australotiphys himonius sp. nov.
Figures 10, 13–22

Material Examined

Holotype

♂, small spring near Roper River on road to Moroak, Northern Territory, Australia [ca. 14°50'S,



Figures 11–12 *Australotiphys magnisetus* Cook, holotype ♂: 11, dorsal aspect; 12, ventral aspect. Scale line = 100 μ m.

133°35'E], 5 July 1987, M.S. Harvey, A.L. Yen (NMV K866; SL).

Paratypes

Australia: Northern Territory: 1♀, same data as holotype (NMV K867; SL). **Queensland:** 1♀, creek 13 km W. of Paluma on road to Hidden Valley, 19°00'S, 146°06'E, 8 July 1986, M.S. Harvey, P.J. Vaughan (NMV K868; SL).

Diagnosis

Tibia and metatarsus of male leg IV with thickened setae. Male and female with ventral shield extending from coxae; glandularia lg1, vg3 and vgx situated in ventral shield.

Description

Adult

Colour pale yellow. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and 6 pairs of ventroglanularia; lg1 and vg3 situated in ventral shield (Figures 14, 17). Dorsum (Figures 13, 16): with 2 pairs of dorsalia posterior to the postocularia. Venter (Figures 14, 17): coxae fused into single plate; apodemes of coxa I nearly extending to posterior edge of coxa III; coxae I fused in mid-line; suture lines between coxae III and IV not reaching mid-line, extending laterally; sclerotized area present posterior to the coxae extending nearly to posterior level of genital field. Genital region (Figures 15, 18): 9–10 pairs of

circular acetabula; 4 (♂), 3 (♀) pairs of small setae present on anterior portion of acetabular plates. Chelicera not examined. Pedipalp (Figure 22): tibia with 2 ventral setae situated in tubercles, and a single distal, medial seta. Legs (Figures 19–21): unmodified; without swimming setae, but with long, often thick, setae on many segments; male tibia and metatarsus IV with several expanded setae.

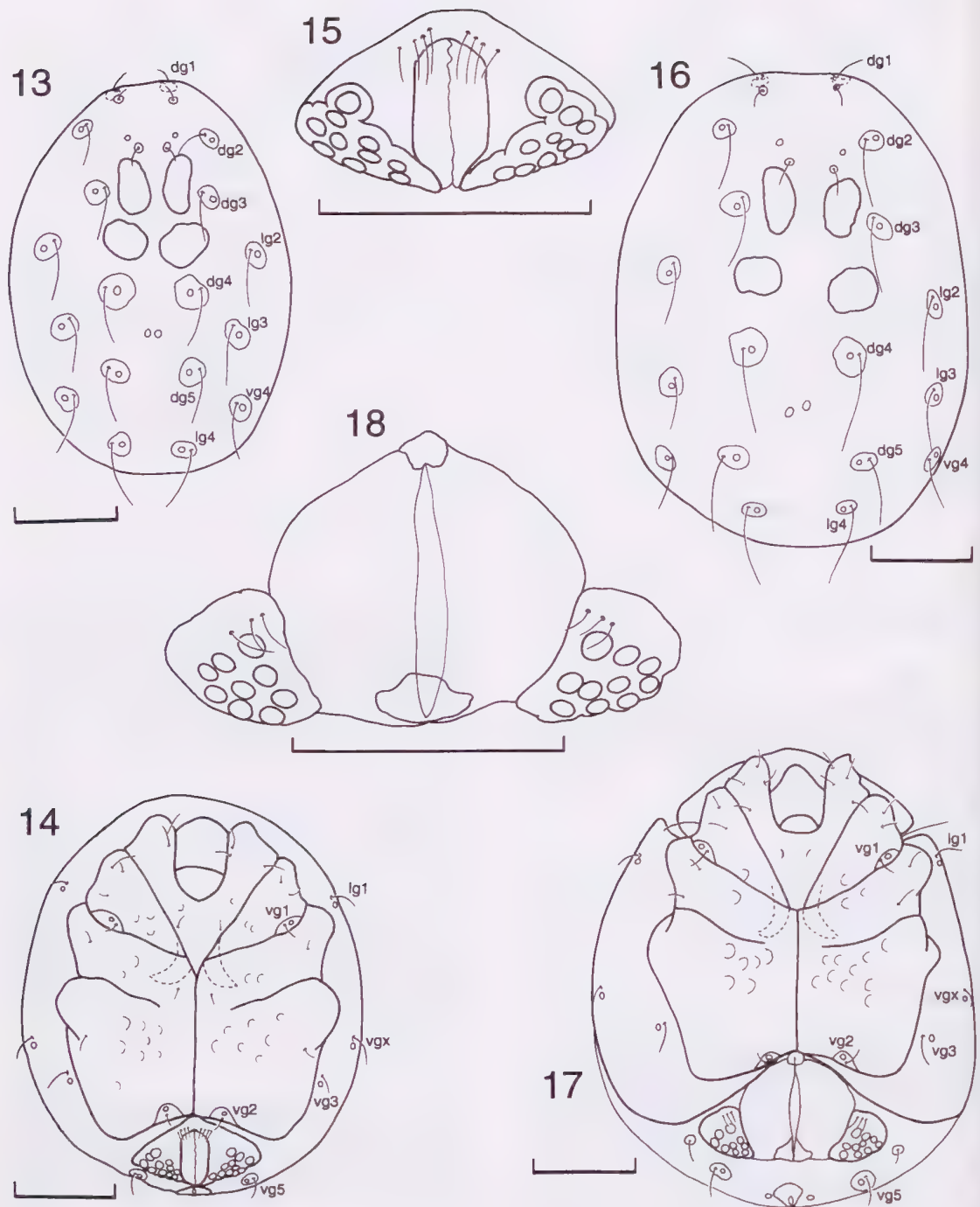
Dimensions (μ m), ♂ (♀): body 381/283 (461–480/339–384); capitulum length 68 (64); genital field 71/118 (115–122/158–192). Pedipalp: trochanter 23 (22), femur 72 (70–72), patella 33 (30–33), tibia 81 (80–84), tarsus 30 (30–32). Leg I: trochanter 51 (48), femur 59 (54–56), patella 86 (77–80), tibia 128 (105–111), metatarsus 143 (126–128), tarsus 128 (118–124). Leg IV: trochanter 72 (69), femur 68 (69), patella 86 (81–89), tibia 84 (110–114), metatarsus 87 (123–127), tarsus 161 (128–132).

Remarks

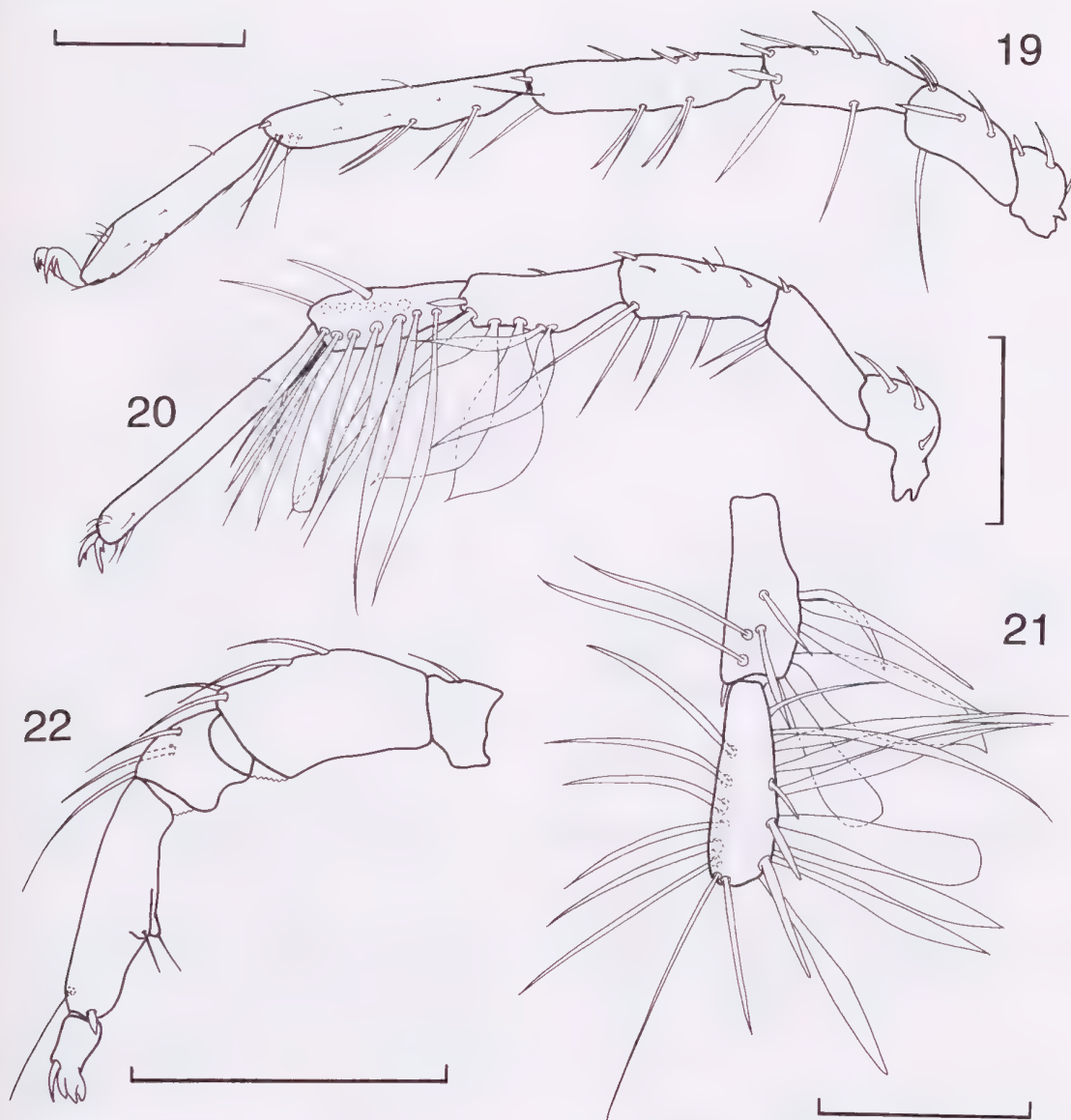
This widespread species (Figure 10) is very similar to *Australotiphys magnisetus*, but males differ in the position of lg1 and vg3. In *A. himonius* they are situated on the sclerotized area above the coxae, whereas in *A. magnisetus* they lie free in the integument.

Etymology

The specific epithet is loosely derived from the name of the type locality (*himonia* Greek, rope of a well).



Figures 13–18 *Australotiphys himonius* sp. nov.: 13–15, holotype ♂: 13, dorsal aspect; 14, ventral aspect; 15, genital field; 16–18, paratype ♀: 16, dorsal aspect; 17, ventral aspect; 18, genital field. Scale lines = 100 µm.



Figures 19–22 *Australotiphys himonius* sp. nov., holotype ♂: 19, left leg I; 20, left leg IV; 21, right tibia and metatarsus IV, ventral aspect; 22, right pedipalp. Scale lines = 100 μ m.

Australotiphys barmutai sp. nov.

Figures 10, 23–31

Material Examined

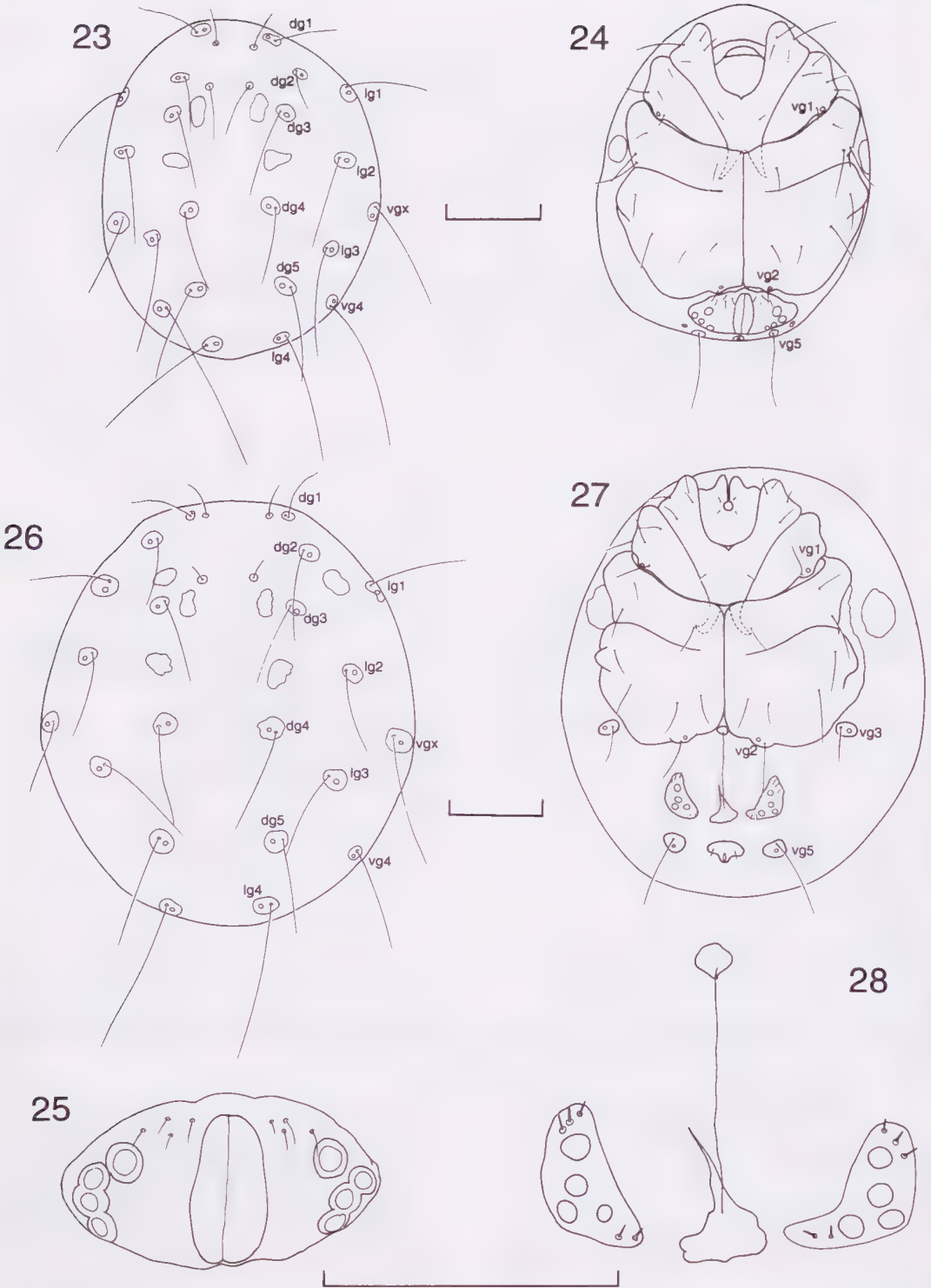
Holotype

♂, Margaret River on Great North Road, Western Australia, Australia, 33°53'S, 115°18'E, 1–2 September 1985, M.S. Harvey, T.J. Doeg (WAM 94/2003; SL).

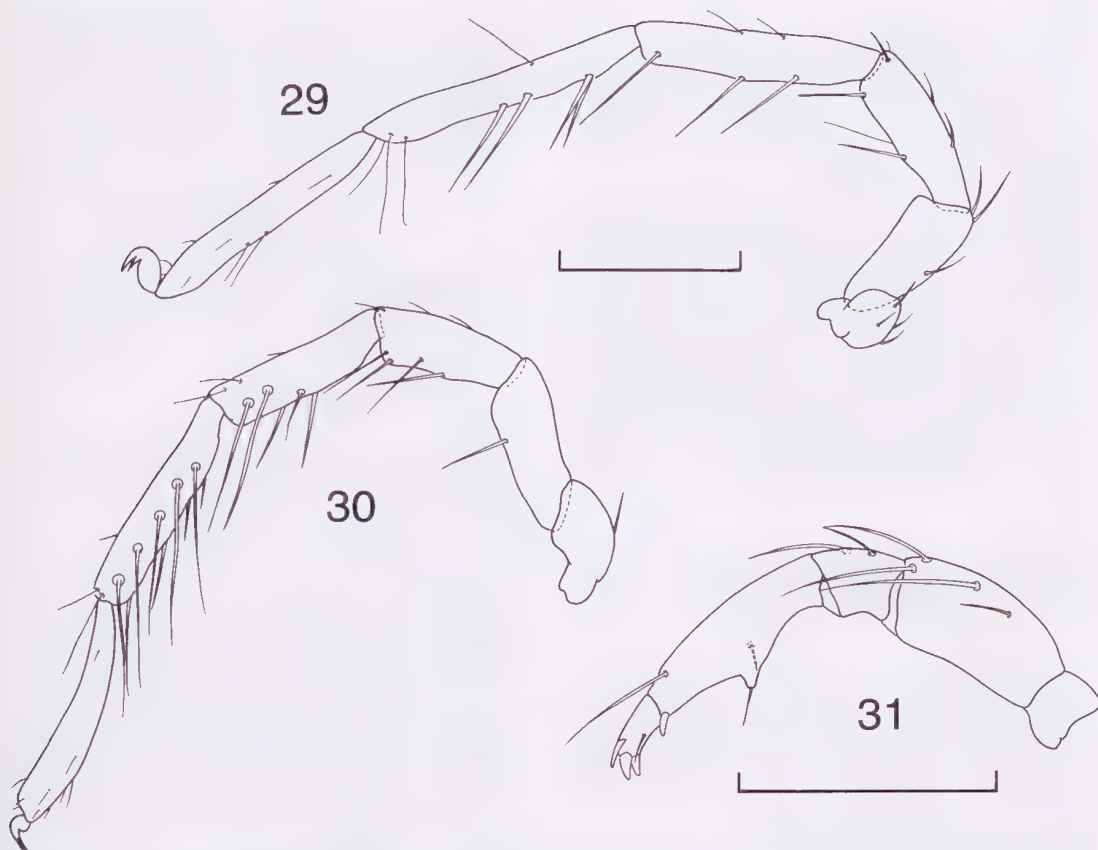
Paratypes

Australia: Western Australia: 18♂, 21♀, 3

deutonymphs, same data as holotype (WAM 94/2004–2045; SL, FL); 6♂, 6♀, 1 deutonymph, same data as holotype (NMV; FL); 2♂, 2♀, same data as holotype (ANIC; FL); 2♂, 2♀, same data as holotype (DCC; FL); 2♂, 2♀, same data as holotype (CNC; FL); 1♀, same data as holotype except 27 August 1987, M.S. Harvey, J.D. Blyth (NMV K891; FL); 4♂, 6♀, Serpentine River below Serpentine Falls, Serpentine Falls Natl Park, 32°23'S, 116°04'E, 24 August 1987, M.S. Harvey, J.D. Blyth, L.A. Barmuta (WAM 94/2046–2055; FL).



Figures 23–28 *Australotiphys barmutai* sp. nov.: 23, dorsal aspect, holotype ♂; 24–25, paratype ♂: 24, ventral aspect; 25, genital field; 26–28, paratype ♀: 26, dorsal aspect; 27, ventral aspect; 28, genital field. Scale lines = 100 μm.



Figures 29–31 *Australotiphys barmutai* sp. nov., holotype ♂: 29, right leg I; 30, right leg IV; 31, right pedipalp. Scale lines = 100 μ m.

Other Material

Australia: Western Australia: 1♀, Barrabup Pool near Nannup [33°57'S, 115°41'E], 1 September 1985, M.S. Harvey, T.J. Doeg (NMV K1019; SL); 1♂, The Cascades, 8 km SSW. of Pemberton, 34°30'S, 116°00'E, 2 September 1985, M.S. Harvey, T.J. Doeg (NMV K1005; SL); 3♂, 10♀, same data except 29 August 1987, M.S. Harvey, J.D. Blyth (NMV K1006–1018; FL); 19♂, 5♀, 2 deutonymphs, same data except 3 May 1990, M.S. Harvey, J.M. Waldock (WAM 94/2056–2081; FL); 2♂, 1♀, Gardner R. at Chesapeake Rd, 34°48'S, 116°11'E, 1 May 1990, M.S. Harvey, J.M. Waldock (WAM 94/2082–2084; FL); 6♂, 1♀, Dog Pool on Shannon River, 20 km S. of Shannon, 34°46'S, 116°22'E, 29 August 1987, M.S. Harvey, J.D. Blyth (WAM 94/2085–2091; FL); 12♂, 21♀, 1 deutonymph, same data except 27–30 April 1990, M.S. Harvey, J.M. Waldock (WAM 94/2092–2125; FL); 3♂, 25♀, 2 deutonymphs, Lake Yeagarup, 18 km SW. of Pemberton, 34°33'S, 115°43'E, 29 August 1987, M.S. Harvey, J.D. Blyth (WAM 94/2126–2155; FL); 11♂, 8♀, same data except 3 May 1990, M.S. Harvey, J.M. Waldock (WAM 94/2156–2174; FL).

Diagnosis

Tibia and metatarsus of male leg IV without thickened setae. Ventral shield absent; 2 pairs of lateralialia.

Description

Adult

Colour pale brown-yellow. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and 6 pairs of ventroglandularia; ventral shield absent (Figures 24, 27). Dorsum (Figures 23, 26): with 2 pairs of dorsalia posterior to the postocularia. Venter (Figures 24, 27): coxae not fused into single plate; apodemes of coxa I nearly extending to posterior edge of coxa III; coxae I fused in mid-line; suture lines between coxae III and IV not reaching mid-line, extending laterally; sclerotized area not present posterior to the coxae; 2 pairs of lateralialia. Genital region (Figures 25, 28): 4 pairs of circular acetabula; each acetabular plate with 4 small setae on anterior portion (♂), or 3 anterior and 2 posterior small setae. Chelicera not examined. Pedipalp (Figure 31): tibia with 2 ventral

setae situated in tubercles, and a single distal, medial seta. Legs (Figures 29–30): unmodified; tibiae and metatarsi with 1–4 very slender swimming setae, and with long, often thick, setae on many segments; male leg IV without thickened setae.

Dimensions (μm), ♂ (♀): body 378–394/294–314 (381–467/332–390); capitulum length 71–83 (70–80); genital field 70/99–115 (90–108/128–140). Pedipalp: trochanter 19–22 (21–22), femur 75–80 (79–81), patella 34–42 (37–42), tibia 82–93 (90–102), tarsus 27–31 (31–33). Leg I: trochanter 45–48 (45–49), femur 61–62 (58–63), patella 90–97 (92–93), tibia 123–133 (120–125), metatarsus 145–156 (138–147), tarsus 132–148 (124–138). Leg IV: trochanter 65 (71–73), femur 90–103 (74–75), patella 78–84 (93–94), tibia 96–102 (127–134), metatarsus 118–128 (141–147), tarsus 126–128 (131–142).

Deutonymph

Much as in adults except that *vgx* is absent; genital region with 2 pairs of acetabula.

Dimensions (μm): body 301/270.

Remarks

Australotiphys barmutai differs from its two congeners by the lack of a ventral shield and by the lack of expanded setae on male leg IV. Under these criteria it is clearly the most plesiomorphic species of the genus. *A. barmutai* appears to be restricted to southwestern Australia (Figure 10).

Etymology

This species is named for Leon Barmuta, intrepid collector of many freshwater invertebrates.

Acercella Lundblad

Acercella Lundblad, 1941: 119; K.O. Viets, 1987: 15.

Type species

Acercella falcipes Lundblad, 1941, by original designation.

Diagnosis

Leg III of male with tarsus swollen and with dissimilar claws; leg IV of male with metatarsus with a large, dorsal or dorso-distal blade extending over tarsus. Body of male with accessory sclerotization near genital field. Genital field with 3 pairs of acetabula. Excretory pore surrounded by sclerotized ring.

Remarks

The addition of a second species to this endemic Australian genus necessitates the alteration of the generic diagnosis provided by Cook (1974). In particular, the shape of coxae IV of the male: in *A.*

falcipes the fourth coxae are nearly triangular, and the posterior margin of the coxal plate is virtually v-shaped (Figure 33); in *A. poorginup* the fourth coxae are rectangular, and the posterior margin of the coxal plate is transverse (Figure 43).

Acercella falcipes Lundblad

Figures 32–41, 52

Acercella falcipes Lundblad, 1941: 119; Lundblad, 1947: 66, figs 43a–f; K. Viets, 1956: 424; Cook, 1974: figs 1175–1176, 1190.

Material Examined

Holotype

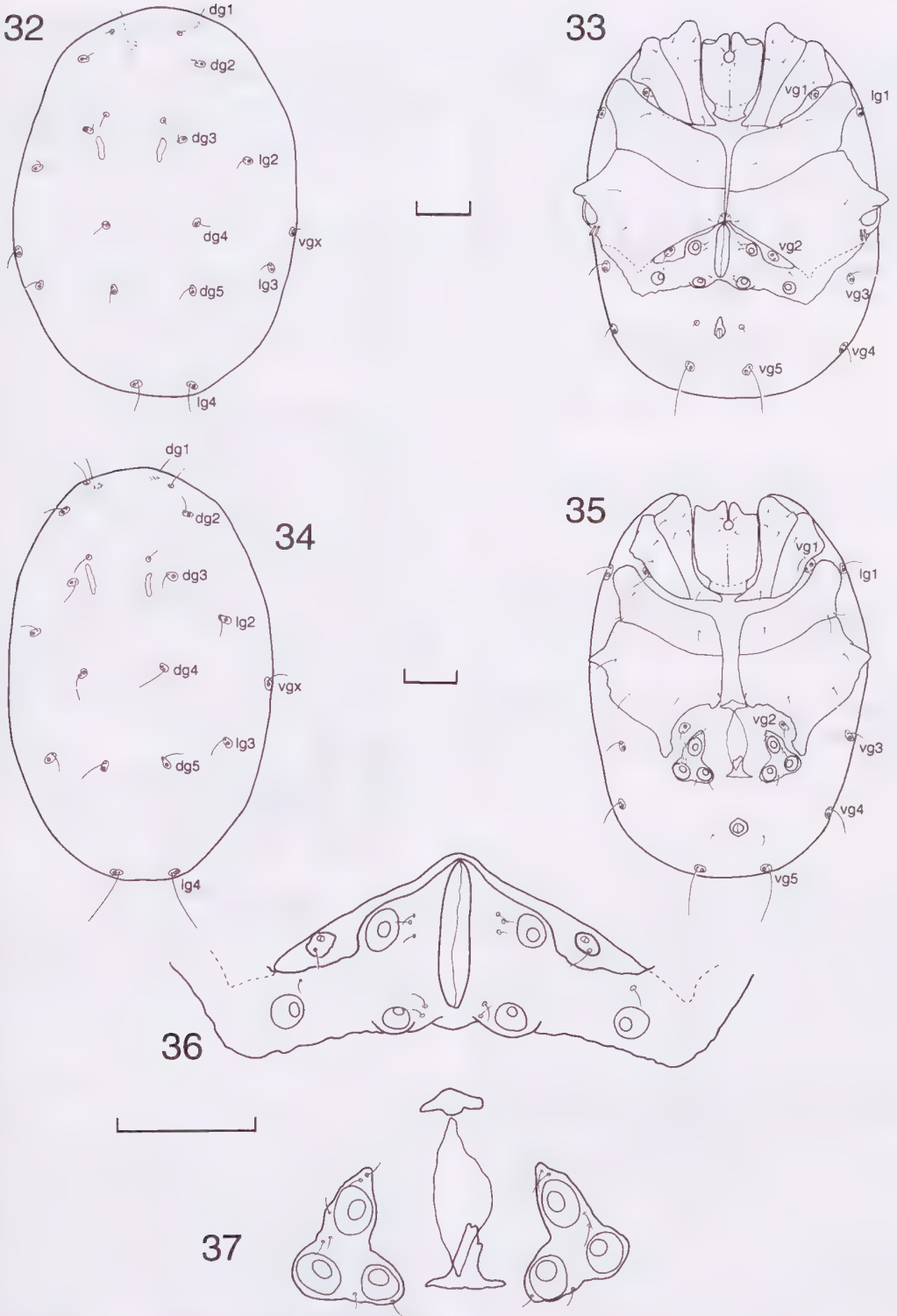
♂, Kalgoorlie, Western Australia, Australia [30°45'S, 121°28'E], cement dam, 14 January 1937, F. Linder (SMNH no. 2939; SL).

Other Material

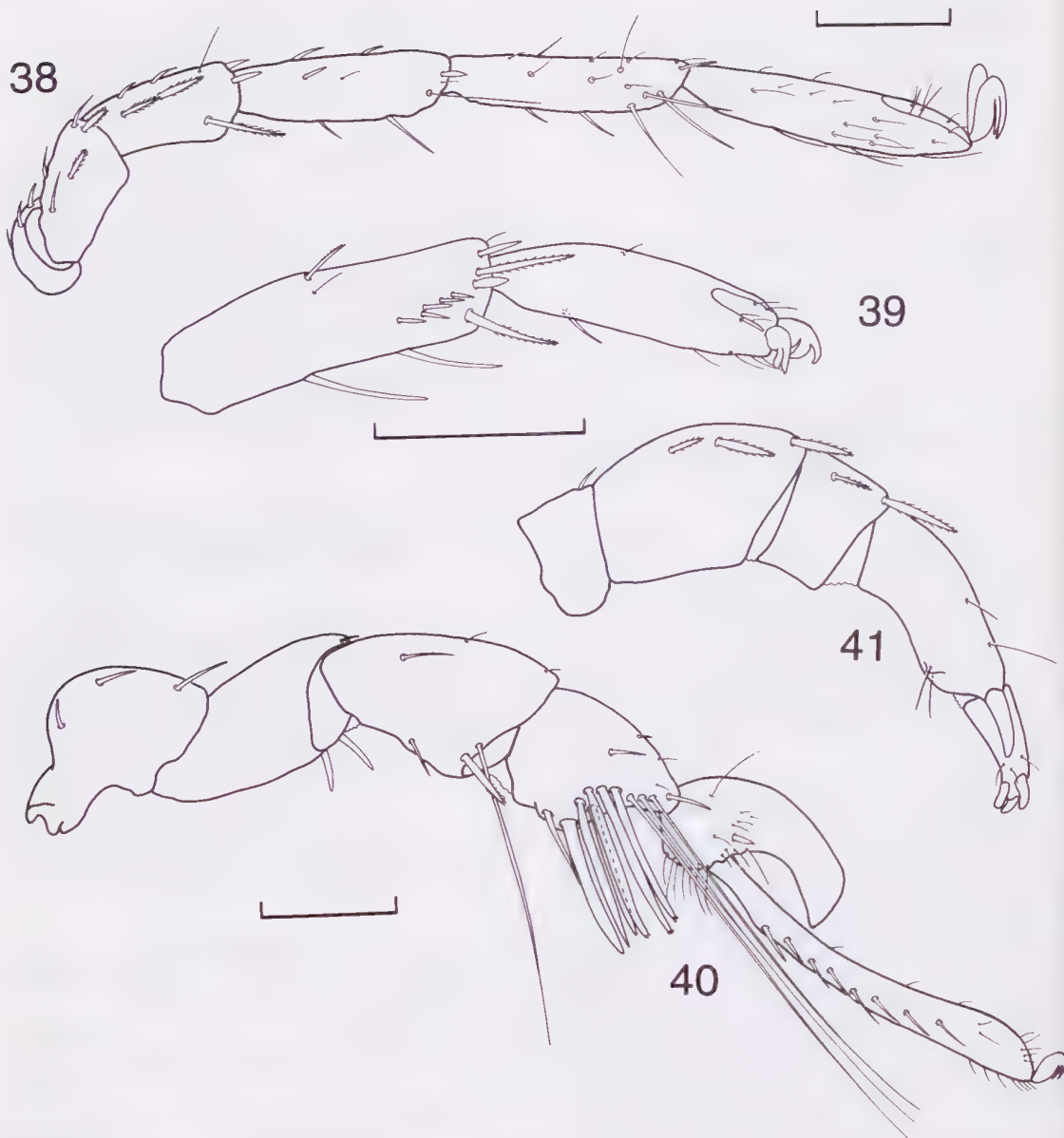
Australia: Victoria: 2♂, 2♀, 117 deutonymphs, swamp on Delegate River, Tea Tree Flat, 37°15'S, 148°50'E, 6 April 1985, D. Cook, M.S. Harvey, A. Boulton (NMV; SL; FL); 1♂, 4♀, Lake Lalbert, near Kerang [35°40'S, 143°19'E], 20 January 1989, S. Fleming (WAM; FL); 22♀, Meyers Creek at Raywood [36°32'S, 144°12'E], 27 September 1985, C. Yule (NMV; FL); 3♂, 3 deutonymphs, Meyers Creek, 4 km WNW. of Raywood [36°30'S, 144°10'E], 5 November 1985, M.S. Harvey, B.J. Scott, L.A. Hoare (NMV; SL); 1 ♀ (labelled as allotype by Lundblad), Mt Macedon [37°23'S, 144°35'E], 27 September 1936, F. Linder (SMNH no. 3401; SL); 6♀, Tragowel Swamp, near Kerang [35°49'S, 143°57'E], 7 June 1989, S. Fleming (WAM; FL). **Western Australia:** 1♀, 1 deutonymph, lakes on Boat Harbour Road, 8 km WSW. of Parryville, 35°01'S, 117°07'E, 30 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/3010–3011; FL); 1♀, Lake Pleasant View, 4 km NE. of Manypeaks, 34°50'S, 118°11'E, 2 September 1987, M.S. Harvey, J.D. Blyth (NMV; FL); 18♂, 6♀, swamp in Melaleuca Park, 31°42'S, 115°57'E, 25 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/2990–3002, NMV; SL; FL); 11♂, 14♀, North Lake, Perth, 32°05'S, 115°49'E, 21 August 1987, M.S. Harvey (1♂, 1♀ each in DCC, CNC, remainder in WAM 88/3003–3009, NMV; FL); 2♂, same locality, January 1986, S. Rolls (WAM 88/3012–3013; FL); 1♀, 2 deutonymphs, Wallaroo Rock, 8 km N. of Wallaroo Siding [30°48'S, 120°29'E], 23 August 1985, M.S. Harvey, T.J. Doeg, R. Marchant (NMV; SL); 1♂, Thompson Lake [32°09'S, 155°50'E], south end, 30 August 1985, M.S. Harvey, T.J. Doeg, B. Murley (NMV; SL).

Diagnosis

Pedipalpal tibia with 2 small ventral setiferous



Figures 32–37 *Acercella falcipes* Lundlad: 32, dorsal aspect, ♂; 33, ventral aspect, ♂; 34, dorsal aspect, ♀; 35, ventral aspect, ♀; 36, genital field, ♂; 37, genital field, ♀. Scale lines = 100 µm.



Figures 38–41 *Acercella falcipes* Lundlad, ♂: 38, right leg I; 39, right leg III, metatarsus and tarsus; 40, right leg IV; 41, left pedipalp. Scale lines = 100 μ m.

tubercles. Male metatarsus IV with dorsal blade-like expansion very thick.

Description

Adult

Colour yellow-brown, legs reddish. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia

present (Figures 32–35). Dorsum (Figures 32, 34): with a pair of poorly defined dorsalia. Venter (Figure 33, 35): apodemes of coxae I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV antero-laterally. Genital region (Figures 36, 37): 3 pairs of large, equally sized acetabula. Chelicera not examined. Pedipalp (Figure 41): tibia with 2 disto-ventral setae set in small tubercles, and with

disto-dorsal seta; tarsus with 4 disto-dorsal setae. Legs (Figures 38–40): ♂ tarsus III with shortened and thickened tarsus, and with unequal claws, posterior claw shortest (Figure 39); ♂ metatarsus III with row of spatulate setae on postero-distal margin; ♂ patella and tibia IV thickened, tibia with 6 stout forward-projecting thick setae on postero-ventral margin; ♂ metatarsus IV with large, thick protuberance extending over tarsus, about one-third as long as tarsus, concave edge of metatarsus with several small spinules (Figure 40); legs II, III and IV with swimming setae arranged as follows: leg II: ♂, tibia 2–4, metatarsus 2–3; ♀, tibia 2–4, metatarsus 4; leg III: ♂, patella 0–2, tibia 6–8, metatarsus 0; ♀, patella 0–2, tibia 4–5, metatarsus 5; leg IV: ♂, patella 0–1, tibia 3–5; ♀, patella 0–3, metatarsus 5–7, tarsus 6–8.

Dimensions (µm), ♂ (♀): body 565–710/455–586 (730–1064/518–604); capitulum length 147–173 (179–195); chelicera length 200 (?); genital field 118–134/288–294 (159–243/248–346). Pedipalp: trochanter 38–43 (41–50), femur 89–103 (106–121), patella 44–56 (58–65), tibia 80–105 (111–122), tarsus 60–71 (65–72). Leg I: trochanter 70–88 (77–83), femur 71–90 (82–96), patella 99–121 (128–135), tibia 141–163 (179–189), metatarsus 147–180 (197–205), tarsus 192–230 (202–250). Leg III: metatarsus 160–200, tarsus 127–144. Leg IV: trochanter 138–160 (128–149), femur 108–134 (110–125), patella 138–186 (173–186), tibia 122–163 (224–232), metatarsus 130–147 (250–261), tarsus 237–288 (237–275).

Deutonymph

Much as in adults except that *v*_{gx} is absent; genital region with 2 pairs of acetabula.

Dimensions (µm): body 448/352.

Remarks

Lundblad (1941 and several other papers) did not make valid holotype designations or restriction of type localities for many species, and there is some doubt as to the type status of the female specimen from Mt Macedon, Victoria which he had labelled as the allotype. As this locality was not mentioned in the original publication, I treat it as not part of the type series, which is restricted to the holotype from Kalgoorlie.

Males of *A. falcipes* differ from those of *A. poorginup* by the shape of the fourth leg and the lack of sclerotization posterior to the genital field. Both males and females differ by the lack of ventral setiferous tubercles on the pedipalpal tibia. *Acercella falcipes* is a remarkably widespread species (Figure 52), and only slight differences in size could be detected between eastern and western populations. The distribution conforms quite well to a Bassian distribution, and the species may eventually be found in suitable habitats in Tasmania.

During August 1987, several pairs collected from North Lake, W.A., were transferred to watch-glasses in the laboratory where mating was observed. The male approached the female and, with their ventral surfaces in contact, he clasped the female's fourth leg between the tarsus and the distal extension of the tarsus of his fourth leg. He then collected the spermatophore from his gonopore with his cupped third tarsi, and transferred it into the female's gonopore. These constitute the first observations on mating in the genus.

Acercella poorginup sp. nov.

Figures 42–52

Material Examined

Holotype

♂, Poorginup Swamp, Western Australia, Australia, 34°33'S, 116°44'E, 4 September 1985, M.S. Harvey, T.J. Doeg (WAM 88/2943; SL).

Paratypes

Australia: Western Australia: 1♂, 1♀, same data as holotype (WAM 88/2944–2945; SL); 1♂, 1♀, same data as holotype (NMV K896–897; SL).

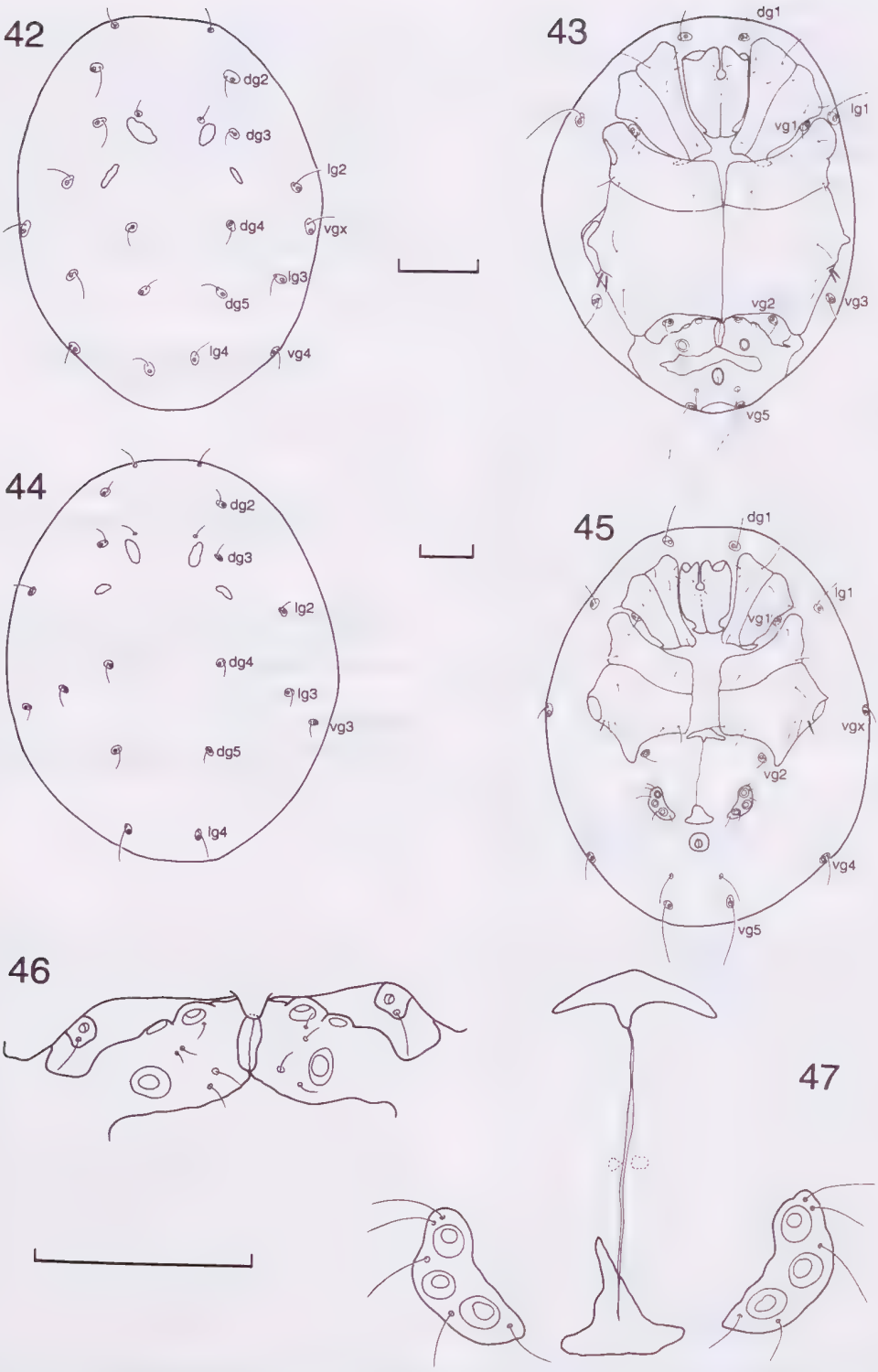
Diagnosis

Pedipalpal tibia with 2 large ventral setiferous tubercles. Male metatarsus IV with dorsal blade-like expansion very thin.

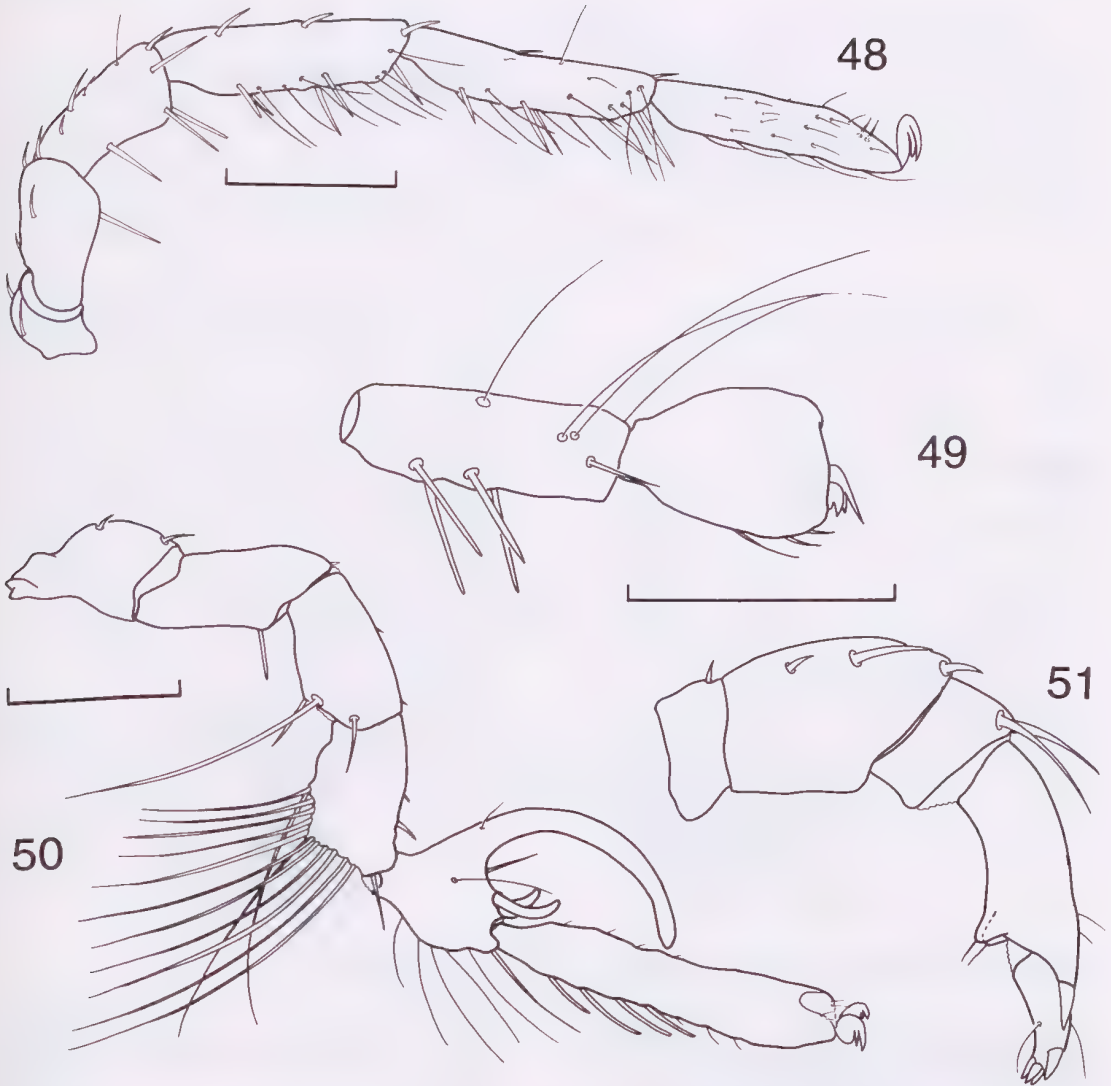
Description

Adult

Colour deep red. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia present (Figures 42–45). Dorsum (Figures 42, 44): with 2 pairs of dorsalia, anterior pair larger than posterior pair. Venter (Figures 43, 45): apodemes of coxa I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV extending laterally (♂) or antero-laterally (♀). Genital region (Figures 46, 47): 3 pairs of acetabula; those of ♂ unequal in size, the posterior pair larger than remaining pairs; those of ♀ virtually in a straight line. Chelicera not examined. Pedipalp (Figure 51): tibia with 2 large disto-ventral setiferous tubercles, and with disto-dorsal seta; tarsus with 4 disto-dorsal setae. Legs (Figures 48–50): ♂ tarsus III extremely shortened and thickened, and with unequal claws, posterior claw shortest (Figure 49); ♂ tibia and metatarsus IV modified, tibia with fan-shaped arrangement of swimming hairs on ventral surface, and metatarsus with large dorsal extension curving over tarsus,



Figures 42–47 *Acercella poorginup* sp. nov.: 42, dorsal aspect, holotype ♂; 43, ventral aspect, holotype ♂; 44, dorsal aspect, paratype ♀; 45, ventral aspect, paratype ♀; 46, genital field, holotype ♂; 47, genital field, paratype ♀. Scale lines = 100 µm.



Figures 48–51 *Acercella poorginup* sp. nov., holotype ♂: 48, right leg I; 49, right leg III, metatarsus and tarsus; 50, right leg IV; 51, left pedipalp. Scale lines = 100 µm.

disto-dorsal end with 2 stout, blunt, slightly curved setae (Figure 50); legs II, III and IV with swimming setae arranged as follows: leg II: ♂, tibia 3, metatarsus 2–3; ♀, tibia 3, metatarsus 3; leg III: ♂, patella 2, tibia 5–6, metatarsus 2–3; ♀, patella 2, tibia 4, metatarsus 4; leg IV: ♂, patella 1, tibia 10–13; ♀, patella 1, metatarsus 5–8, tarsus 5–7.

Dimensions (µm), ♂ (♀): body 512–544/365–390 (774–781/621–659); capitulum length 121–134 (135–141); genital field 52/142 (173–185/196–198). Pedipalp: trochanter 30–35 (33–34), femur 86–93 (91–95), patella 41–49 (43–49), tibia 94–102 (104–111), tarsus 55–62 (64–68). Leg I: trochanter 64–69 (62), femur 70–79 (58–67), patella 100–108 (87–95),

tibia 153–164 (135–147), metatarsus 150–167 (140–147), tarsus 152–167 (142–149). Leg III: metatarsus 111–113, tarsus 81–83. Leg IV: trochanter 100–113 (96–99), femur 94–98 (84–95), patella 94–102 (108–122), tibia 101–117 (154–172), metatarsus 84–92 (172–188), tarsus 211–221 (157–173).

Remarks

Acercella poorginup differs from *A. falcipes* by possessing two large setiferous tubercles on the pedipalpal tibia. Males further differ by the shape of the fourth leg and by the presence of sclerotization posterior to the genital field.

At present, this species has been collected only in



Figure 52 Map of Australia showing known distributions of *Acercella* and *Piona* spp.

Poorginup Swamp, W.A. (Figure 52). I revisited the type locality during August 1987, and found that the swamp had dried to a muddy quagmire which apparently sustained no macroinvertebrate fauna. Limited attempts were made to dig into the mud to ascertain whether nymphal mites had moved down into the hyporheion, but these proved unsuccessful. Due to the clearing of the natural vegetation around the swamp for farmland, there is a serious threat that if the swamp does refill at a later date, it could simply refill with saline water, as has at least one other lake in the Lake Muir complex (of which Poorginup is the smallest and most pristine). Like *Pseudohydryphantes doegi* Harvey (Harvey 1987), *Acercella poorginup* has not been collected at any other site, despite a fairly large collecting effort in the southwest over recent years, and it is possible that both species are extinct.

This species has recently been placed on

Schedule 1 of the Protected Invertebrate Fauna under the Wildlife Conservation Act 1950 (Minson 1994).

Etymology

The specific epithet is a noun in apposition taken from the type locality.

Subfamily Pioninae Thor

Piona Koch

Nesaea Koch, 1836: 21. Junior homonym of *Nesaea* Leach, 1814 (Crustacea) and *Nesaea* Risso, 1826 (Mollusca). Type species: *Nesaea rosea* Koch, 1836, by subsequent designation of Koch (1842).

Piona Koch, 1842: 13; K.O. Viets, 1987: 605. Type species: *Nesaea ovata* Koch, 1836 (junior subjective synonym of *Nesaea variabilis* Koch,

1836), by subsequent designation of Koch (1842).

Curvipes Koenike, 1891: 20. Replacement name for *Nesaea* Koch, 1836. Synonymised by Wolcott (1905).

Piona (*Dispersipiona*) K. Viets, 1926: 194. Type species: *Hydrachna clavicornis* Müller, 1776, by original designation. Synonymised by Cook (1960).

Piona (*Tetrapiona*) K. Viets, 1926: 194. Type species: *Nesaea variabilis* Koch, 1836, by original designation. Synonymised by Cook (1960).

Piona (*Carnepiona*) Besseling, 1959: 22. Type species: *Nesaea carnea* Koch, 1836 by original designation. Synonymised by Cook (1974).

Piona (*Pusillopiona*) Besseling, 1959: 22. Type species: *Nesaea pusilla* Neuman, 1875 by original designation. Synonymised by Cook (1974).

Piona (*Conglopiona*) Besseling, 1959: 22. Type species: *Nesaea conglobata* Koch, 1836 by original designation. Synonymised by Cook (1974).

Diagnosis

Male tarsus III with dissimilar claws; tibia IV of male with concavity lined with small, blunt setae. Body without accessory sclerotization. Genital field with many pairs of acetabula. Excretory pore surrounded by sclerotized ring.

Remarks

Due to the large number of described *Piona* species, and a certain amount of variation within the genus, several authors have erected subgenera. The history and status of these names was summarized by Cook (1974) who noted that their use was hazardous due to gradations between species. Smith (1976) adopted a more reasonable approach, and erected a series of species-group categories.

***Piona cumberlandensis* (Rainbow)**

Figures 52–54

Atax cumberlandensis Rainbow, 1906: 160, fig. 37 (in part).

Unionicola cumberlandensis (Rainbow): Walter, 1928: 59; K. Viets, 1956: 360.

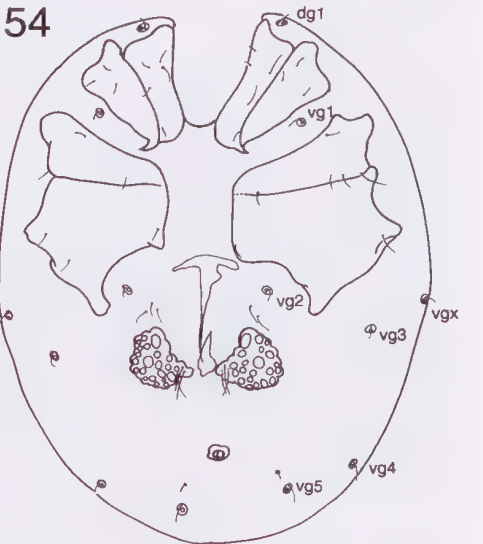
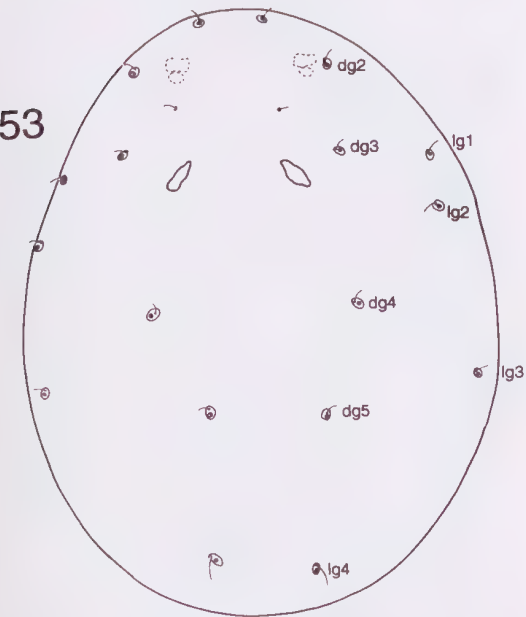
Unionocola [sic] *cumberlandensis* (Rainbow): K. Viets, 1932: 364;

Unionicola (*Hexatax*) *cumberlandensis* (Rainbow): Halík, 1941: 103.

Piona uncatiformis Lundblad, 1941: 118. Synonymized by Cook (1986).

Piona (*Piona*) *uncatiformis* Lundblad: Lundblad, 1947: 69, figs 44a–i; K. Viets, 1956: 460.

Piona cumberlandensis (Rainbow): Cook, 1986: 201, figs 1053–1058, 1061.



Figures 53–54 *Piona cumberlandensis* (Rainbow), ♀: 53, dorsal aspect; 54, ventral aspect. Scale line = 100 µm.

Unionicola (Unionicola) cumberlandensis (Rainbow): Vidrine, 1986: 234.

Material Examined

Lectotype of Atax cumberlandensis

♂ (present designation), Parramatta, New South Wales, Australia [33°48'S, 151°01'E], ponds, 12 June 1905, [A.R. McCulloch] (AM KS15751; FL, SL).

Paralectotypes of Atax cumberlandensis

Australia: New South Wales: 1♂, 7♀, same data as lectotype (AM KS15751; FL, SL).

Lectotype of Piona uncatiformis

♂ (designated by Lundblad (1947), see below), North Portland, Victoria, Australia [38°19'S, 141°35'E], dam, 26 November 1936, F. Linder (SMNH no. 2953; SL).

Paralectotypes of Piona uncatiformis

Australia: Victoria: 1♂, Shepparton [36°23'S, 145°24'E], May 1925, E.J. Semmens (SMNH no. 3404; SL); 1♂, 1♀, Lake Kariah [38°11'S, 143°13'E], 24 November 1936, F. Linder (SMNH no. 3403, 3405; SL).

Other Material

Australia: New South Wales: 1 ♀ (labelled 'allotypus' by Lundblad), Deniliquin [35°32'S, 144°57'E], 5 October 1936, F. Linder (SMNH no. 3402; SL); 1♂, 2♀, Lake Willeroo, 30°05'S, 145°18'E, 28 March 1989, B.V. Timms (WAM; SL); 6♂, 14♀, Newcastle [32°56'S, 151°46'E], 24 September 1986, B.V. Timms (NMV; FL); 9♀, 3 deutonymphs, Shortland Wetlands Centre bird pond, near Newcastle [32°53'S, 151°41'E], 19 March 1987, B.V. Timms (NMV; FL). **Northern Territory:** 8♂, 2♀, Kurundi Waterhole, Murchison Range [20°30'S, 134°40'E], 7 August 1979, J.D. Blyth (NMV; FL); 2♀, creekpool no. 2, Palm Valley, Finke Gorge Natl Park [24°03'S, 132°42'E], 26 July 1979, J.D. Blyth (NMV; FL); 1♀, Big Hole Ellery Gorge Nature Park [23°47'S, 133°04'E], 23 July 1979, J.D. Blyth (NMV; FL); 15♂, 19♀, same data (NMV; FL). **South Australia:** 1♀, Brighton [35°01'S, 138°31'E], 6 March 1957 (SAM N19901303; SL). **Tasmania:** 6♂, 8♀, Big Waterhouse Lake, via Bridport [40°54'S, 147°37'E], 31 January 1990, B. V. Timms (WAM; FL); 2♀, Big Waterhouse Lake [40°54'S, 147°37'E], 9 October 1991, TJK, LFM (QVM; FL); 1♂, 2♀, same locality, 15 January 1992, TJK, LFM (QVM; FL); 1♂, same locality, 18 March 1992, TJK, LFM (QVM; FL); 2♀, same locality, 15 January 1992, LFM, JG (QVM; FL); 5♀, same locality, 15 July 1992, LFM, PLP (QVM; FL); 1♀, Blackmans Lagoon [40°55'S, 147°36'E], 21 January 1992, LFM, PLP (QVM; FL);

2♂, 8♀, Bowlers Lagoon [40°52'S, 147°55'E], 23 September 1991, TJK, LFM (QVM; FL); 1♀, same locality, 6 November 1991, TJK, LFM (QVM; FL); 3♂, 6♀, 1 deutonymph, same locality, 14 January 1992, TJK, LFM (QVM; FL); 2♂, 3♀, same locality, 17 March 1992, TJK, LFM (QVM; FL); 5♀, same locality, 14 July 1992, PLP, LFM (QVM; FL); 11♀, Cambridge [42°50'S, 147°26'E], 30 July 1966, E. Aves, A.J. Dartnall (TM; FL); 2♂, 1♀, Cape Naturaliste [40°51'S, 148°44'E], 13 January 1992, TJK, LFM (QVM; FL); 5♀, same locality, 13 July 1992, L. McGowan, P. LaPalombara (QVM; FL); 8♀, Lake Leake [42°01'S, 147°50'E], November 1937, J.W. Evans (TM; FL); 52♂, 65♀, 1 deutonymphs, 1 teliophan, Lake Pedder [ca. 42°54'S, 146°05'E], various dates, P.S. Lake (NMV; FL); 1♀, Little Waterhouse Lake [40°53'S, 147°36'E], 15 August 1991, TJK, LFM (QVM; FL); 3♀, same locality, 9 October 1991, TJK, LFM (QVM; FL); 3♀, same locality, 18 March 1992, LFM, JKG (QVM; FL); 1♀, South Hobart [42°54'S, 147°18'E], 26 November 1985, J. Barclay (TM; FL). **Victoria:** 2♀, Acheron River at Old Coach Road, pond near river, 37°30'S, 145°41'E, 5 March 1987, M.S. Harvey (NMV; FL); 2♂, 5♀, Barwon River, E. branch of Lake Elizabeth, 12 km S. of Forrest [ca. 38°34'S, 143°45'E], 31 August 1975, J. Aldenhoven (NMV; FL); 1♀, same data, except 1975 (NMV; FL); 1♀, Black Flat, Wyperfeld Natl Park [35°35'S, 142°02'E], 6 April 1974, J.D. Blyth (NMV; FL); 1♀, Expedition Pass Reservoir, 1.5 km SW. of Faraday [37°03'S, 144°16'E], 5 November 1985, M.S. Harvey, B.J. Scott, L.A. Hoare (NMV; FL); 4♀, Lake Albacutya [35°45'S, 141°58'E], 9 September 1977 (NMV; FL); 8♀, Lake Modewarre [38°15'S, 144°09'E], 28 September 1966, D. Pollard (NMV; FL); 6♂, 1♀, Melba Gully Park near Laver's Hill, 30°42'S, 143°22'E, 21 May 1986, M.S. Harvey, P.J. Vaughan (NMV; FL); 4♂, 3♀, Ryan's I Billabong, 5 km E. of Albury [36°06'S, 147°58'E], 15 January 1988, R. Butcher (NMV; FL); 1♀, same data except 19 January 1988 (NMV; FL); 5♂, 13♀, 6 larvae, Shaws Lake, NE. of Blackwood [ca. 37°29'S, 144°19'E], 8 January 1986, M.S. Harvey, R. St Clair (NMV; FL); 3♂, same data except M.S. Harvey, M. Blossfelds, G.H. Southwell, C. Southwell (NMV; FL); 6♀, Snowden's Billabong, near Wodonga [36°06'S, 147°58'E], 18 February 1985 (NMV; FL). **Western Australia:** 1♀, Abydos-Woodstock Reserve, Nganaloongana Pool, 21°36'S, 118°48'E, 28 October 1990, M.S. Harvey (WAM; FL); 2♂, Bilung Pool, Congo Creek, Gascoyne Junction-Geraldton Road [25°42'S, 116°00'E], 11 November 1979, J.D. Blyth (NMV; FL); 1♀, The Cascades, 8 km SSW. of Pemberton, 34°30'S, 116°00'E, 29 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/3026; FL); 9♂, 13♀, larvae, North Lake, Perth, 32°05'S, 115°49'E, 21 August 1987, M.S. Harvey (WAM 88/3027-3036, NMV; FL).

Diagnosis

Male genital field with deep, central pit, and with 2 large acetabula and many small acetabula; female genital field with acetabula lying on 2 large plates, each plate with 2 large acetabula and many small acetabula. Pedipalpal tibia with distal thickened seta. Anterior claw of male tarsus III strongly modified.

Description*Adult*

See Cook (1986). Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia and 6 pairs of ventroglandularia (Figures 53–54).

Deutonymph

Much as in adults except that vxg is absent; genital region with 2 pairs of acetabula.

Remarks

The type material of *Atax cumberlandensis* also contains an adult specimen of *Hydrodroma monticola* (Piersig) (Hydrodromidae), and thus a lectotype of *A. cumberlandensis* is designated.

The original description of *Piona uncatiformis* by Lundblad (1941) was very brief; he simply mentioned male characters and referred to '♂' from 'Australien, Victoria'. No holotype was designated, and no specific type locality was mentioned. Subsequently, Lundblad (1947) published a more extensive redescription and referred to a 'Typus', an 'Allotypus' from New South Wales, and to various localities in Victoria from which other specimens had been collected. As no holotype was mentioned in the original publication, I have considered that the types from Victoria should be regarded as syntypes [Article 72a of the International Code of Zoological Nomenclature (third edition)], but that the restriction by Lundblad (1947) of a 'Typus' can be construed as designation of a lectotype under Article 74b of the Code. The remaining specimens from Victoria are treated as paralectotypes, but the 'allotype' from New South Wales is excluded from the type series.

The synonymy of *Piona uncatiformis* with *A. cumberlandensis* by Cook (1986) is confirmed by comparison of the type series of both species. *Piona cumberlandensis* is widely distributed in Australia (Figure 52). It belongs to the *Piona coccinea* group as defined by Smith (1976).

Mating was observed between males and females of this species during August 1987, after specimens had been taken from North Lake, W.A., and placed in watch-glasses. The female hooked her pedipalps over the tibiae IV of the male whilst upside-down. The male then transferred the spermatophore from his genital aperture to the female's aperture by cupping it between his modified tarsi III.

Piona australica K.O. Viets

Figures 52, 55–66

Piona australica K.O. Viets, 1980: 164, figs 25–31.

Types (not examined)*Holotype*

♂, Lake Hume, Albury, New South Wales, Australia [ca. 36°10'S, 147°05'E], 13 December 1977, R. Shiel (VC).

Paratypes

Australia: New South Wales: 4 ♀ (including allotype), same data as holotype (VC); 1 ♀, Boorowa River [ca. 34°10'S, 148°48'E], 10 April 1977, R. Shiel (VC).

Material Examined

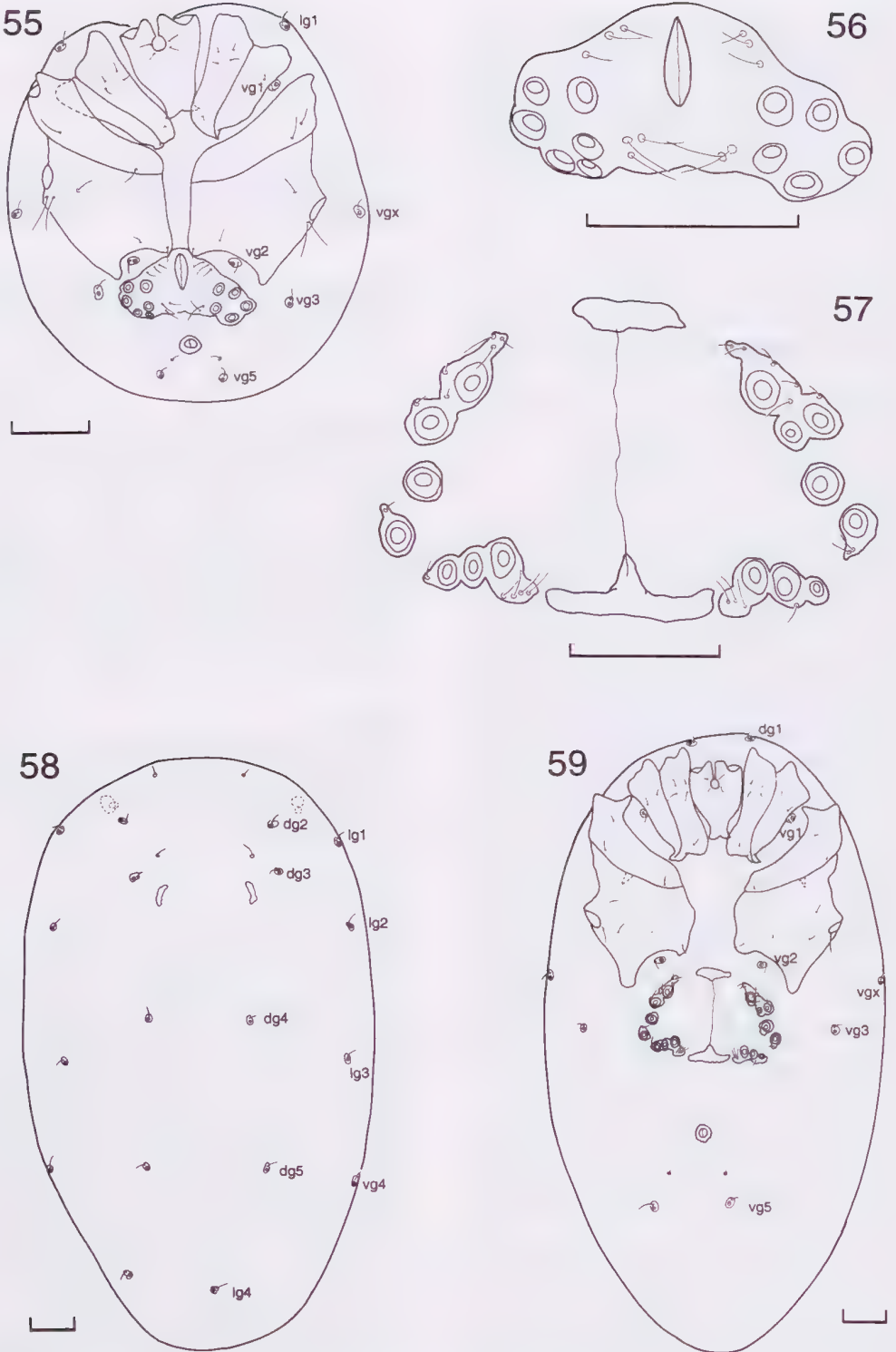
Australia: New South Wales: 12 ♀, Burgess Lagoon via Maitland [ca. 32°44'S, 151°34'E], 13 April 1984, B.V. Timms (NMV; SL, FL); 2 ♂, 8 ♀, 5 deutonymphs, Lake Hume [ca. 36°10'S, 147°05'E], 21 February 1991, V. Matveev (WAM; FL); 2 ♀, Lake McKenzie, Jervis Bay, ca. 35°08'S, 150°43'E, 20 January 1989, B. Timms (WAM; FL). **Western Australia:** 1 ♂, 8 ♀, pools in Rudall River, Great Sandy Desert, ca. 22°20'S, 122°00'E, 23 March 1988, R. Hart (WAM 88/3014–3018, NMV; SL, FL).

Diagnosis

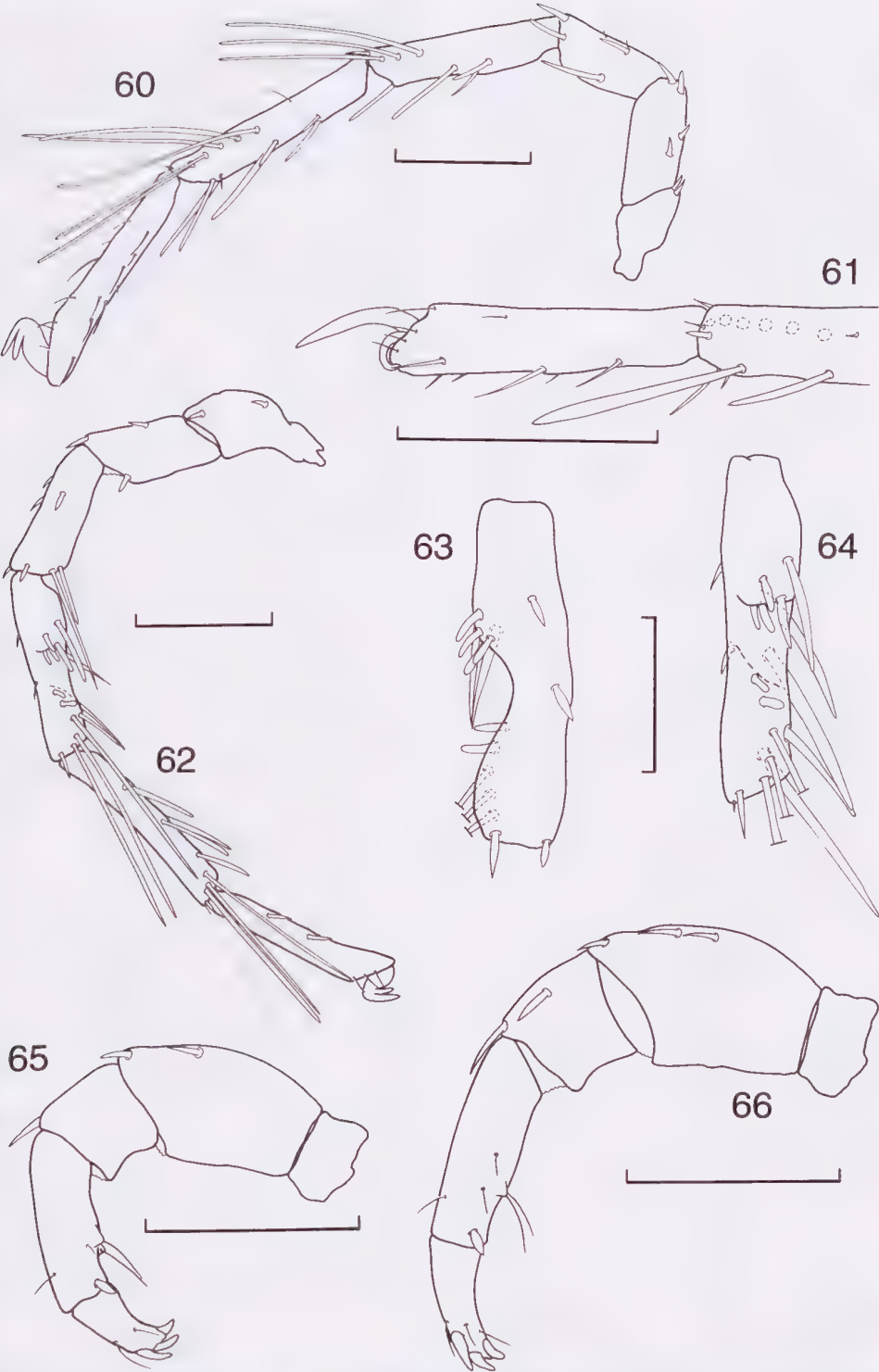
Male genital field without deep, central pit; female genital field with acetabula lying on small, scattered plates. Pedipalpal tibia with stout, distal seta. Anterior claw of male tarsus III strongly curved, without ventral clawlet.

Description*Adult*

Colour (in alcohol) pale yellow. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia (Figures 55, 58, 59). Dorsum (Figure 58): with a single pair of dorsalia. Venter (Figures 55, 59): apodemes of coxa I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV extending antero-laterally. Genital region (Figures 56, 57): 5–6 (♂), 5–8 (♀) pairs of acetabula; those of ♂ all lying on acetabular plate, acetabula unequal in size, the posterior pair larger than remaining pairs; those of ♀ lying on small, scattered plates. Chelicera not examined. Pedipalp (Figures 65, 66): tibia with stout disto-ventral seta; tarsus with 3 disto-dorsal setae. Legs (Figures 60–64): ♂ tarsus III with extremely shortened and thickened tarsus, and with unequal claws, anterior claw shortest, without ventral clawlet (Figure 61); ♂ tibia IV with lateral concavity bearing 4 anterior and 2 posterior



Figures 55–59 *Piona australica* K.O. Viets: 55, ventral aspect, ♂; 56, genital field, ♂; 57, genital field, ♀; 58, dorsal aspect, ♀; 59, ventral aspect, ♀. Scale lines = 100 μ m.



Figures 60–66 *Piona australica* K.O. Viets: 60, left leg I, ♂; 61, right leg III, detail of tarsus and distal portion of metatarsus, ♂; 62, left leg IV, ♂; 63, right tibia IV, dorsal, ♂; 64, left tibia IV, lateral, ♂; 65, left pedipalp, ♂; 66, right pedipalp, ♀. Scale lines = 100 μm.

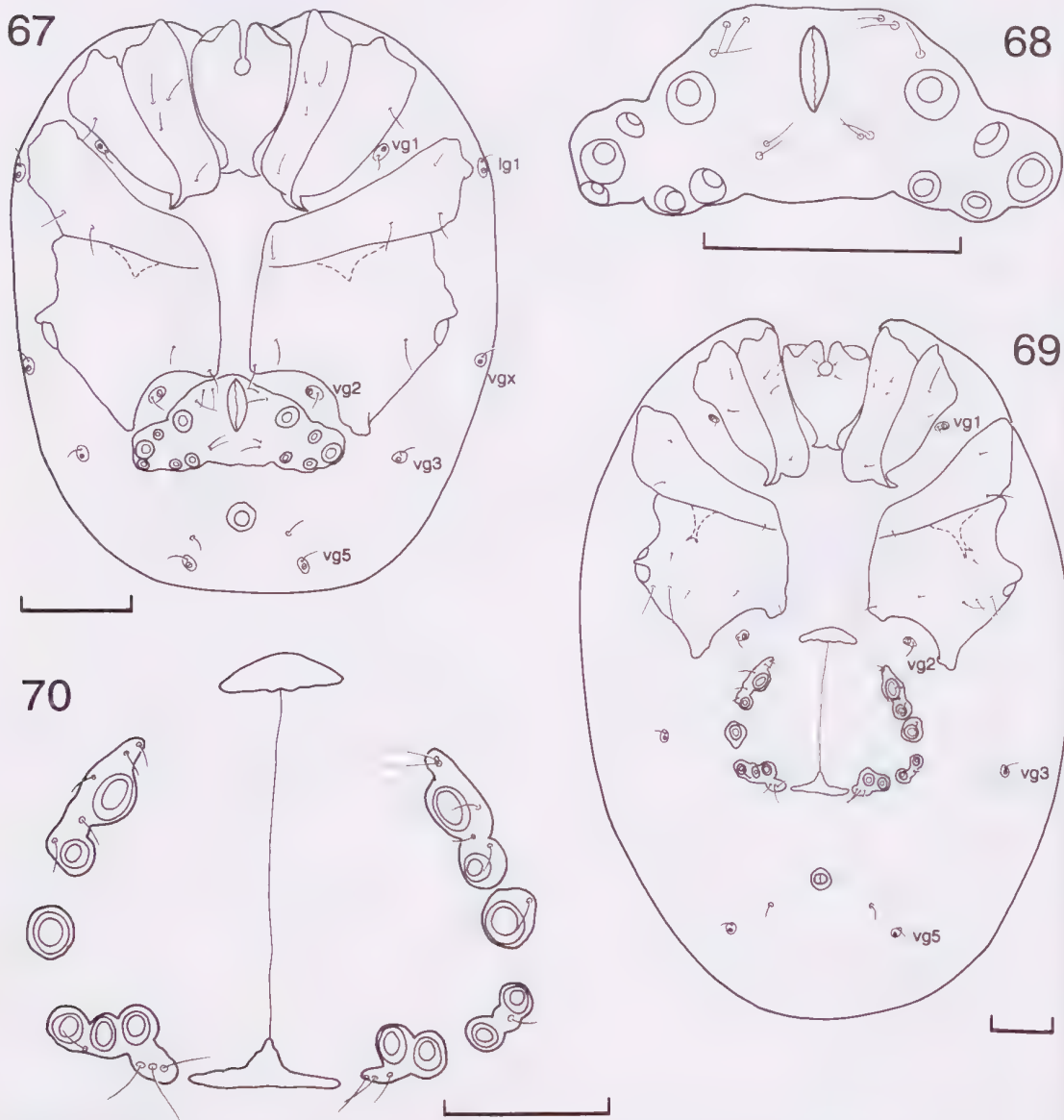
peg-like setae (Figures 63, 64); legs with swimming setae arranged as follows: leg I: ♂, tibia 3, metatarsus 5; ♀, patella 0–2, tibia 6–8, metatarsus 12–14; leg II: ♂, tibia 3, metatarsus 6; ♀, patella 3–6, tibia 10–11, metatarsus 12–14; leg III: ♂, patella 2, tibia 6, metatarsus 5; ♀, patella 5–6, tibia 10–11, metatarsus 12–14; leg IV: ♂, tibia 3, metatarsus 3; ♀, patella 1–2, metatarsus 7–9, tarsus 3–4.

Dimensions (µm), ♂ (♀): body 512/384 (1193–1431/684–859); capitulum length 136 (167–206); genital field 84/175 (237–262/314–403). Pedipalp: trochanter 25 (29–35), femur 99 (103–127), patella

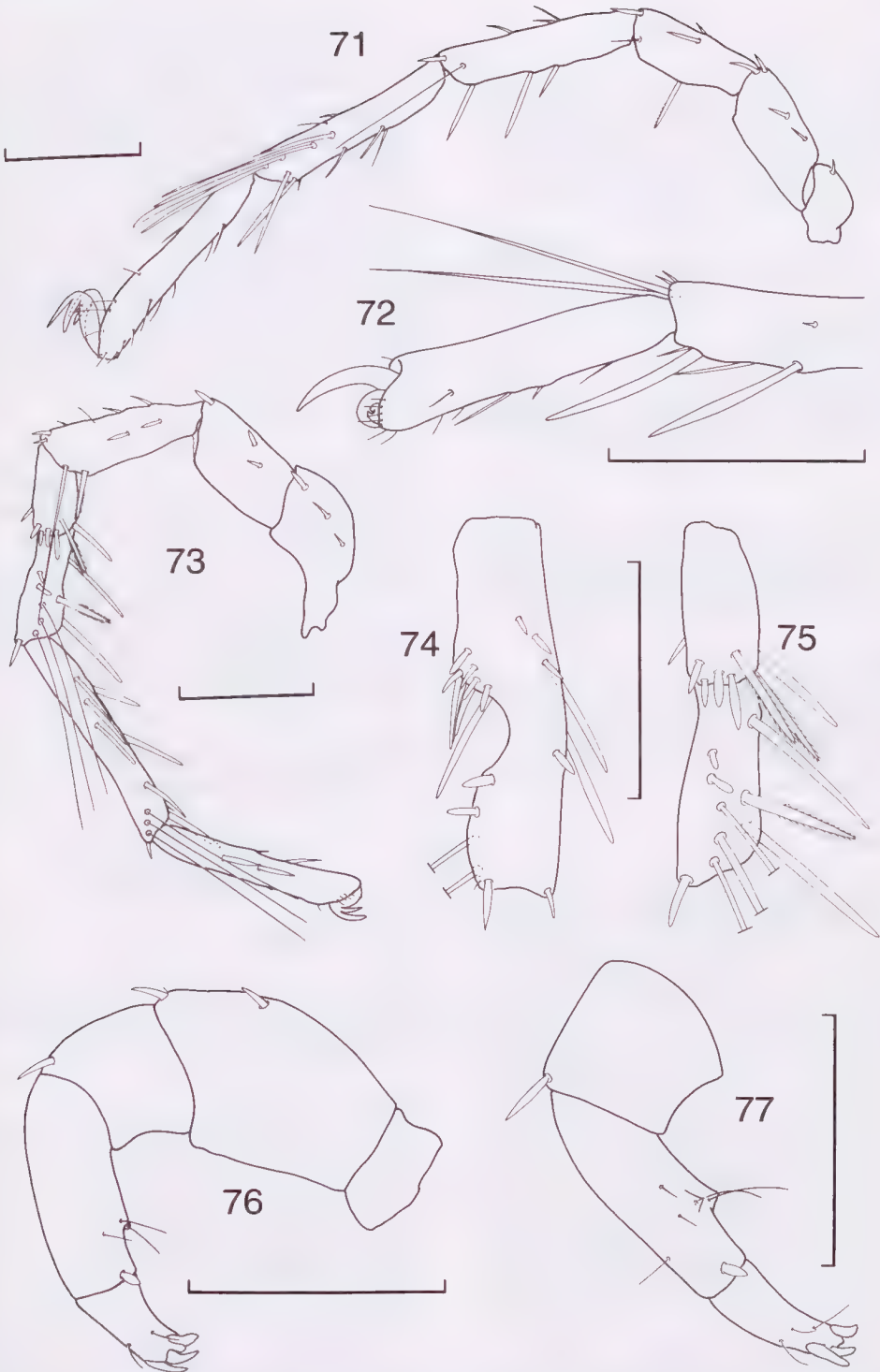
52 (54–63), tibia 88 (92–110), tarsus 52 (65–76). Leg I: trochanter 62 (90–96), femur 83 (115–134), patella 102 (140–154), tibia 147 (192–231), metatarsus 168 (210–268), tarsus 180 (213–273). Leg III: metatarsus 166, tarsus 127. Leg IV: trochanter 110 (122–160), femur 80 (94–132), patella 103 (137–192), tibia 146 (180–259), metatarsus 152 (197–282), tarsus 142 (204–253).

Deutonymph

Much as in adults except that vxg is absent; genital region with 2 pairs of acetabula.



Figures 67–70 *Piona marchanti* sp. nov.: 67–68, holotype ♂: 67, ventral aspect; 68, genital field; 69–70, ♀ paratype: 69, ventral aspect; 70, genital field. Scale lines = 100 µm.



Figures 71–77 *Piona marchanti* sp. nov.: 71, left leg I, holotype ♂; 72, right leg III, detail of tarsus and distal portion of metatarsus, holotype ♂; 73, left leg IV, paratype ♂; 74, right tibia IV, dorsal, paratype ♂; 75, left tibia IV, lateral, paratype ♂; 76, right pedipalp, holotype ♂; 77, right pedipalp (patella, tibia, tarsus), paratype ♀. Scale lines = 100 µm.

Dimensions (μm): body 566/465.

Remarks

Piona australica belongs to the *variabilis* species-group as defined by Smith (1976). It appears to be widely distributed (Figure 52). See under the following species for characters by which *P. australica* and *P. marchanti* may be distinguished.

Piona marchanti sp. nov.

Figures 52, 67–77

Material Examined

Holotype

♂, Coonjimba Billabong, Jabiru Mining Camp, Northern Territory, Australia, 12°42'S, 132°54'E, 15 January 1980, R. Marchant (NMV K874; SL).

Paratypes

Australia: Northern Territory: 2♂, same data as holotype (NMV K875–876, SL, FL); 1♀, Mudginberri Billabong, Jabiru Mining Camp, 12°42'S, 132°54'E, 14 February 1980, R. Marchant (NMV K877; SL).

Diagnosis

Male genital field without deep, central pit; female genital field with acetabula lying on small, scattered plates. Pedipalpal tibia with stout, distal seta. Anterior claw of male tarsus III strongly curved, with ventral clawlet.

Description

Adult

Colour (in alcohol) pale yellow. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia (Figures 67, 69). Dorsum with a single pair of dorsalia. Venter (Figure 67, 69): apodemes of coxa I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV extending antero-laterally. Genital region (Figures 68, 70): 5–8 (♂), 6–7 (♀) pairs of acetabula; those of ♂ all lying on acetabular plate, acetabula unequal in size, the posterior pair larger than remaining pairs; those of ♀ lying on small, scattered plates. Chelicera not examined. Pedipalp (Figures 76, 77): tibia with 2 large disto-ventral setiferous tubercles, and with disto-dorsal seta; tarsus with 3 disto-dorsal setae. Legs (Figures 71–75): ♂ tarsus III with unequal claws, anterior claw strongly curved, with curved ventral clawlet, posterior claw long and slightly curved (Figure 72); ♂ tibia IV modified, with posterior concavity lined with several proximal and 2 distal peg-like setae (Figures 74–75); legs with swimming setae arranged as follows: leg I: ♂, tibia 1–3, metatarsus

4–5; ♀, tibia 6, metatarsus 9; leg II: ♂, tibia 2–6, metatarsus 5; ♀, patella 2, tibia 9, metatarsus 13; leg III: ♂, patella 0–2, tibia 5–6, metatarsus 5; ♀, patella 1, tibia 10, metatarsus 12; leg IV: ♂, patella 2, tibia 3, metatarsus 3; ♀, patella 1, metatarsus 7, tarsus 4.

Dimensions (μm), ♂ (♀): body 557–614/403–429 (896/704); capitulum length 144–149 (179); genital field 80–90/194–214 (259/301). Pedipalp: trochanter 21–29 (?), femur 105–114 (?), patella 56–59 (59), tibia 89–97 (102), tarsus 48–52 (60). Leg I: trochanter 61–70 (83), femur 86–104 (115), patella 100–115 (132), tibia 151–170 (182), metatarsus 166–192 (213), tarsus 179–198 (220). Leg III: metatarsus 172–186, tarsus 125–128. Leg IV: trochanter 113–132 (128), femur 80–90 (108), patella 109–125 (161), tibia 145–159 (200), metatarsus 162–180 (221), tarsus 148–159 (204).

Remarks

Piona marchanti belongs to the *variabilis* species-group (Smith 1976), and is most similar to *P. australica*. It differs by possessing a small, curved ventral clawlet on the posterior claw of leg III (Figure 72) which is lacking in *P. australica*. Females of these two species are apparently indistinguishable. *Piona marchanti* has only been collected from two billabongs in what is now Kakadu Natl Park (Figure 52).

Etymology

This species is named for Richard Marchant, collector of the type specimens.

Piona murleyi sp. nov.

Figures 52, 78–89

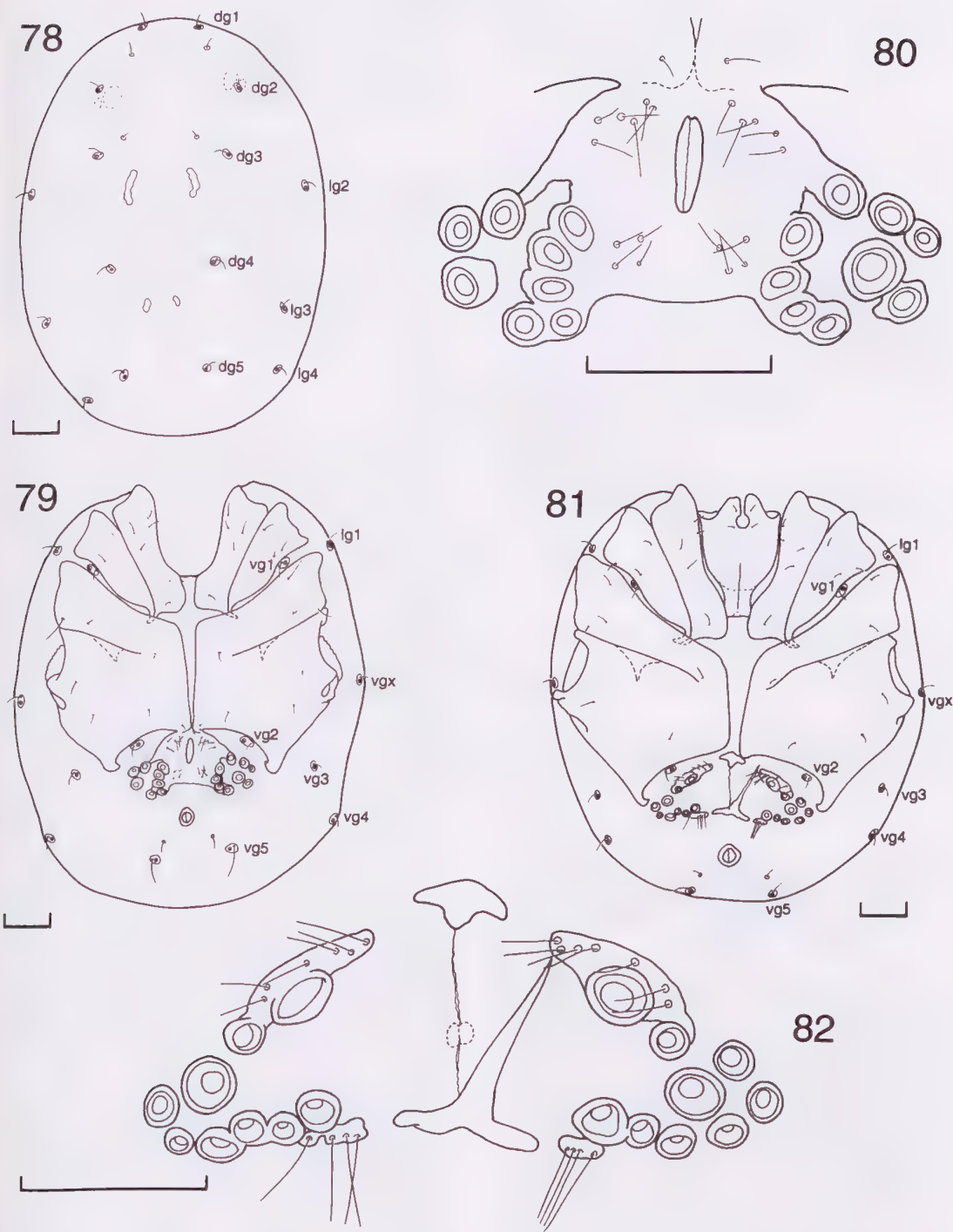
Material Examined

Holotype

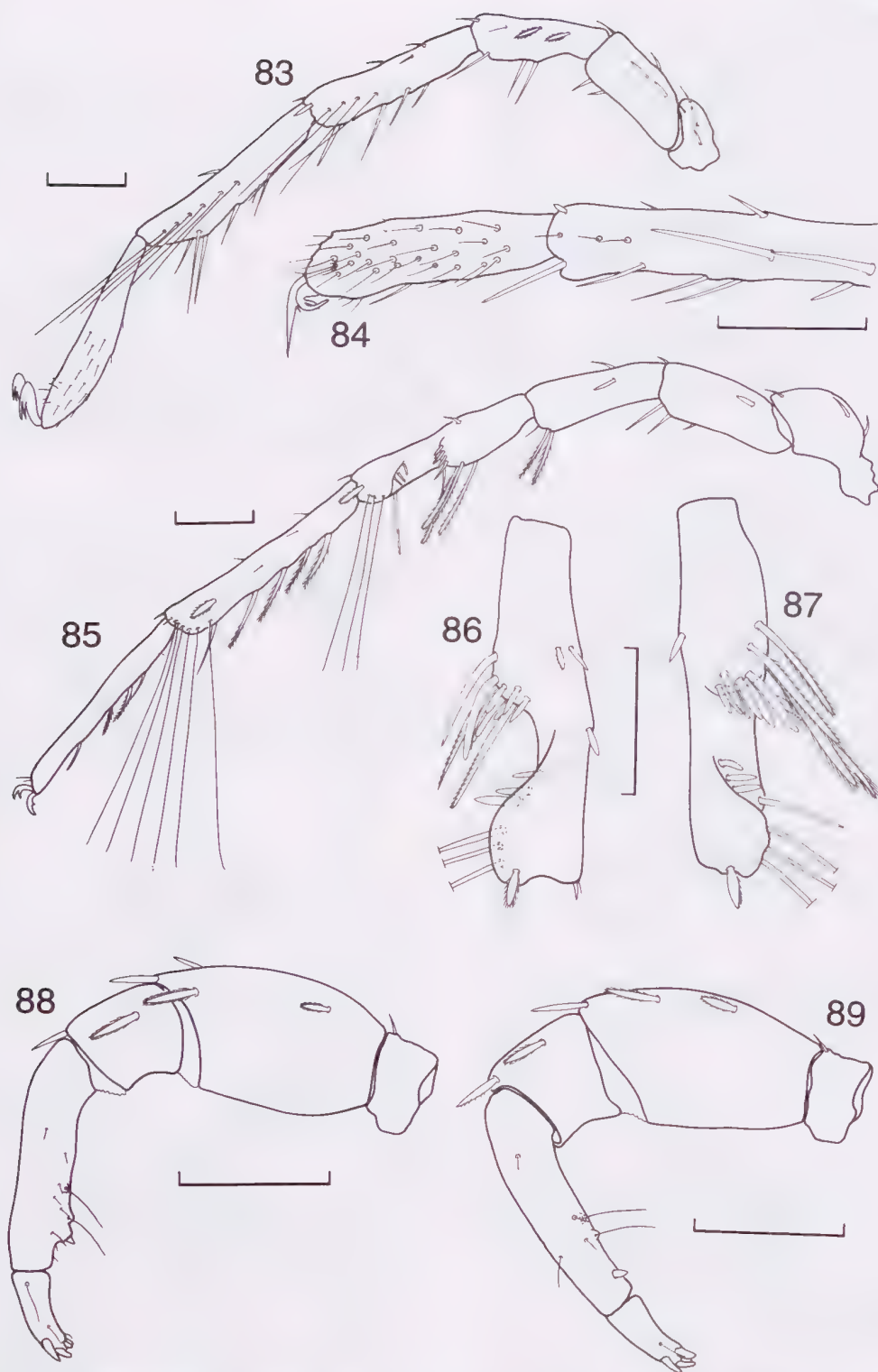
♂, swamp in Melaleuca Park, Western Australia, Australia, 31°42'S, 115°57'E, 25 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/2949; SL).

Paratypes

Australia: Western Australia: 14♂, 9♀, same data as holotype (WAM 88/2950–2955, 2958–2974; SL, FL); 10♂, 7♀, same data as holotype (NMV K881–882, 892, 878–880, 984–994; SL, FL); 2♂, 2♀, same data as holotype (SAM; FL); 2♂, 2♀, same data as holotype (ANIC; FL); 1♂, 1♀, same data as holotype (CNC; FL); 1♂, 1♀, same data as holotype (DCC; FL); 3♂, 5♀, Lake Pleasant View, 4 km NE. of Manypeaks, 34°50'S, 118°11'E, 2 September 1987, M.S. Harvey, J.D. Blyth (WAM 88/2975–2982; FL); 2♂, 5♀, same data (NMV K883–884, 886–890; FL); 2♂, small dam S. of Lake Poorginup, 34°33'S, 116°44'E, 31 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/2956–2957; SL); 1♂, Loch McNess,



Figures 78–82 *Piona murleyi* sp. nov.: 78–80, holotype ♂: 78, dorsal aspect; 79, ventral aspect; 80, genital field; 81–82, paratype ♂: 81, ventral aspect; 82, genital field. Scale lines = 100 µm.



Figures 83–89 *Piona murleyi* sp. nov.: 83, left leg I, holotype ♂; 84, right leg III, detail of tarsus and distal portion of metatarsus, holotype ♂; 85, left leg IV, holotype ♂; 86, right tibia IV, paratype ♂; 87, left tibia IV, holotype ♂; 88, left pedipalp, paratype ♂; 89, right pedipalp, paratype ♀. Scale lines = 100 µm.

Yanchep Natl Park, 31°32'S, 115°40'E, 25 August 1987, M.S. Harvey, J.D. Blyth (WAM 88/2983; FL); 3♂, North Sister Lake, 5 km N. of Manypeaks, 34°48'S, 118°09'E, 2 September 1987, M.S. Harvey, J.D. Blyth (NMV K893-895; FL); 2♂, 4 deutonymphs, Thompson Lake [32°09'S, 155°50'E], 30 August 1985, M.S. Harvey, T.J. Doeg, B. Murley (NMV K999-1004; SL).

Diagnosis

Male genital field without deep, central pit; female genital field with acetabula lying on small, scattered plates. Male pedipalpal tibia with stout, sub-distal seta, set in tubercle; that of female distal, not set in tubercle. Anterior claw of male tarsus III strongly curved, with ventral clawlet.

Description

Adult

Colour pale yellow, legs pale maroon. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia (Figures 78-79, 81). Dorsum (Figure 78): with 2 pairs of dorsalia, anterior pair larger than posterior pair. Venter (Figures 79, 81): apodemes of coxa I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV extending antero-laterally, not reaching mid-line. Genital region (Figures 80, 82): 6-13 (usually 9-10) (♂), 9-14 (usually 9-10) (♀) pairs of acetabula; those of ♂ mostly situated on plate which is attached to coxae; those of ♀ lying on small, scattered plates. Chelicera not unusual. Pedipalp (Figures 88-89): tibia of ♂ with stout ventral seta sub-distal, set in tubercle, of ♀ distal; tarsus with 4 disto-dorsal setae. Legs (Figures 83-87): ♂ tarsus III setose, with slightly shortened and thickened tarsus; claws unequal, anterior claw strongly curved, with ventral clawlet, posterior claw long and nearly straight, with ventral clawlet (Figure 84); ♂ tibia IV modified, with posterior concavity lined with several proximal and 3 (rarely 2) distal peg-like setae (Figures 86-87); legs II, III and IV with swimming setae arranged as follows: leg I: ♂, tibia 3-4, metatarsus 5-6; ♀, tibia 5-8, metatarsus 8-10; leg II: ♂, tibia 4-7, metatarsus 6-7; ♀, tibia 8-10, metatarsus 8-12; leg III: ♂, tibia 5-9; ♀, tibia 10-11, metatarsus 9-12; leg IV: ♂, metatarsus 5-6; ♀, tibia 6-8, metatarsus 6-9.

Dimensions (µm), ♂ (♀): body 659-864/531-704 (859-992/747-827); capitulum length 181-219 (262-276); chelicera length 255-291 (309-331); genital field 116-152/267-304 (138-160/320-351). Pedipalp: trochanter 35-45 (38-51), femur 148-167 (164-182), patella 73-87 (82-96), tibia 143-172 (168-197), tarsus 52-68 (68-77). Leg I: trochanter 77-93 (83-114), femur 93-128 (122-150), patella 134-179 (160-198), tibia 178-237 (230-291), metatarsus 209-

280 (256-330), tarsus 197-278 (254-313). Leg III: metatarsus 232-307, tarsus 127-172. Leg IV: trochanter 139-187 (171-206), femur 109-147 (147-179), patella 154-179 (223-262), tibia 218-250 (293-374), metatarsus 246-314 (312-403), tarsus 211-282 (244-339).

Deutonymph

Much as in adults except that vxg is absent; genital region with 2 pairs of acetabula.

Dimensions (µm): body 614/467.

Remarks

Piona murleyi belongs to the *variabilis* species-group as defined by Smith (1976), and differs from the other species of the group by the position and morphology of the seta on the male pedipalpal tibia. *Piona murleyi* is apparently restricted to southwestern Australia (Figure 52), where it is common in lakes and swamps.

Etymology

This species is named for Brendon Murley, who assisted in the collection of this species at one site.

Piona puripalpis K.O. Viets

Figures 52, 90-100

Piona puripalpis K.O. Viets, 1984: 429, figs 41-45.

Types (not examined)

Holotype

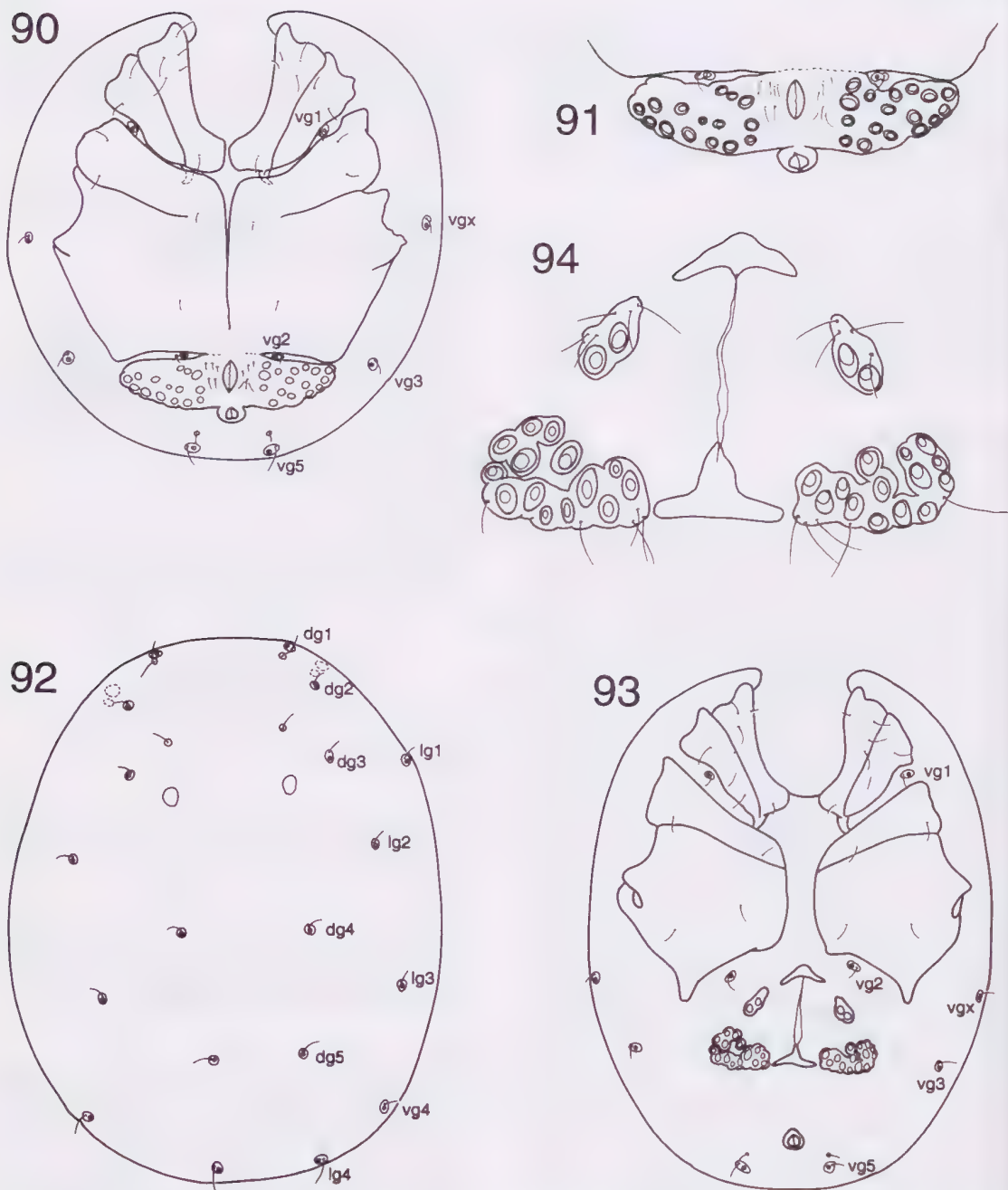
♂, Station Spring, via Mataranka, Roper Valley, Northern Territory, Australia [ca. 14°55'S, 133°04'E], 12 July 1981, B.V. Timms (VC).

Paratype

Australia: New South Wales: 1♀, mining pool no. 11, Crowdy Head via Taree [31°51'S, 152°45'E], 6 September 1980, B.V. Timms (VC).

Material Examined

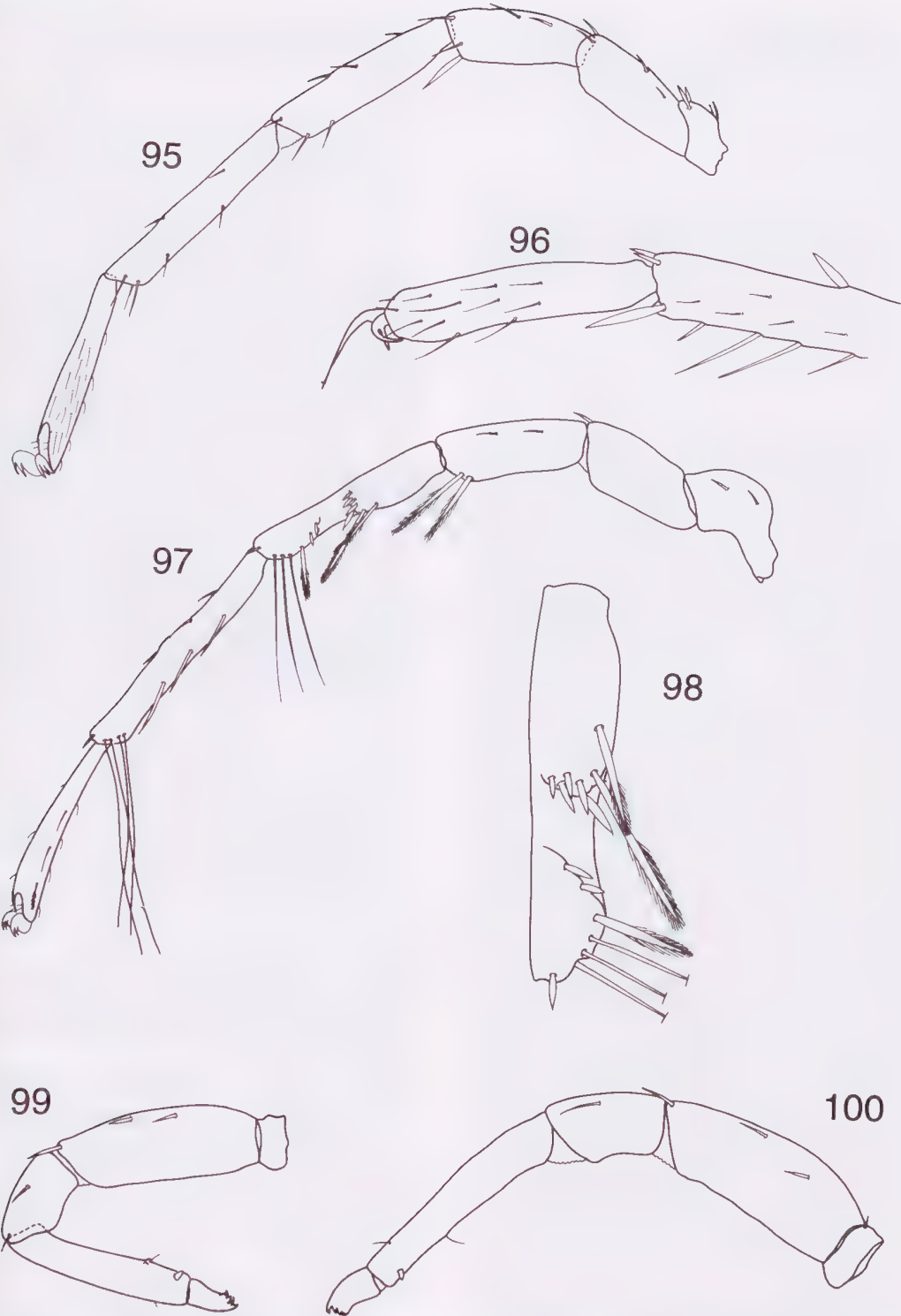
Australia: Northern Territory: 1♀, Coonjimba Billabong, Jabiru Mining Camp, 12°42'S, 132°54'E, 12 June 1979, R. Marchant (NMV; FL); 1♀, same data except 7 August 1979 (NMV; FL); 1♂, same data except 4 September 1979 (NMV; FL); 1♀, Dunlop's Swamp, Katherine Gorge Natl Park [ca. 12°19'S, 132°30'E], 7 July 1987, M.S. Harvey, A.L. Yen (NMV; FL); 1♂, 1♀, billabong on Flying Fox Creek, Kakadu Natl Park [ca. 12°44'S, 132°22'E], 30 June 1987, M.S. Harvey, A.L. Yen (NMV; FL); 7♂, 6♀, Fogg Dam [12°34'S, 131°17'E], 29 June 1987, M.S. Harvey, A.L. Yen (NMV; FL); 16♂, 4♀, same data except 13 July 1987 (NMV; FL); 2♀, Georgetown Billabong, Jabiru Mining Camp, 12°42'S, 132°54'E, 30 April 1979, R. Marchant



Figures 90–94 *Piona puripalpis* K.O. Viets: 90–91, ♂: 90, ventral aspect; 91, genital field; 92–94, ♀: 92, dorsal aspect; 93, ventral aspect; 94, genital field. Scale lines = 100 µm.

(NMV; FL); 1 ♀, same data (NMV; FL); 1 ♂, 1 deutonymph, Goanna Billabong, Jabiru Mining Camp, 12°42'S, 132°54'E, 5 April 1979, R. Marchant (NMV; FL); 3 ♂, 3 ♀, same data except 12 July 1979 (NMV; FL); 1 ♂, same data except 16 January 1980 (NMV; FL); 1 ♂, Jabiluka Billabong, Kakadu Natl

Park [12°28'S, 132°52'E], 3 July 1987, M.S. Harvey, A.L. Yen (NMV; FL); 2 ♂, 8 ♀, larvae, Kapalga Billabong, Kakadu Natl Park [12°36'S, 132°26'E], 2 July 1987, M.S. Harvey, A.L. Yen (NMV; FL); 1 ♀, Malabanbandju Billabong [12°46'S, 132°45'E], 3 July 1987, M.S. Harvey, A.L. Yen (NMV; FL); 4 ♂, 3 ♀,



Figures 95–100 *Piona puripalpis* K.O. Viets: 95–99, ♂: 95, left leg I; 96, right leg III, detail of tarsus and distal portion of metatarsus; 97, left leg IV; 98, left tibia IV, lateral; 99, right pedipalp; 100, right pedipalp, ♀. Scale lines = 100 μ m.

Mudginberri Billabong, Jabiru Mining Camp, 12°42'S, 132°54'E, 13 July 1979, R. Marchant (NMV; FL). **Western Australia:** 4♂, 3♀, billabong on Arthur Ck, 135 km N. of Turkey Creek [16°03'S, 128°21'E], 11 July 1987, M.S. Harvey, A.L. Yen (WAM 88/3019–3025; FL).

Diagnosis

Male genital field without deep, central pit; female genital field with acetabula lying on small, scattered plates. Pedipalpal tibia with small, sub-distal seta. Anterior claw of male tarsus III strongly curved, with ventral clawlet.

Description

Adult

Colour pale blue-green. Glandularia: 5 pairs of dorsoglandularia, 4 pairs of lateroglandularia, and 6 pairs of ventroglandularia present (Figures 90, 92–93). Dorsum (Figure 92): with 1 pair of dorsalia. Venter (Figures 90, 93): apodemes of coxa I very short; suture lines between coxae I and II and coxae III and IV present; suture lines between coxae III and IV extending laterally (♂) or antero-laterally (♀). Genital region (Figures 91, 94): with 14–23 (♂), 11–16 (♀) pairs of acetabula; ♂ genital field fused to posterior margin of coxae IV. Chelicera stout. Pedipalp (Figures 99–100): segments, especially femur and tibia, elongate; tibia with stout, blunt, ventral, sub-distal seta; tibia with 1 indistinct disto-ventral setiferous tubercle, tubercle often absent in ♀; tarsus with 4 disto-dorsal setae. Legs (Figures 95–98): ♂ tarsus III with slightly shortened and thickened tarsus, and with unequal claws, posterior claw long and slender, anterior claw strongly curved with ventral clawlets (Figure 96); ♂ tibia and metatarsus IV modified, with posterior concavity lined with several proximal and 2 distal peg-like setae (Figure 98); legs II, III and IV with swimming setae arranged as follows: leg II: ♂, tibia 0–2, metatarsus 3–4; ♀, tibia 1, metatarsus 4–5; leg III: ♂, patella 0–1, tibia 3–5, metatarsus 5–6; ♀, patella 0–1, tibia 5, metatarsus 6–7; leg IV: ♂, tibia 3, metatarsus 5; ♀, tibia 3–4, metatarsus 5–7.

Dimensions (µm), ♂ (♀): body 531–704/442–499 (819–922/589–608); capitulum length 164–186 (203–212); chelicera length 198 (193); genital field 70–84/249–287 (160–174/256–275). Pedipalp: trochanter 25–27 (29–30), femur 173–198 (202–221), patella 86–103 (107–121), tibia 166–195 (204–218), tarsus 44–52 (54–58). Leg I: trochanter 64–68 (79–86), femur 102–109 (120–128), patella 133–150 (141–167), tibia 175–205 (202–224), metatarsus 211–230 (231–244), tarsus 188–211 (204–216). Leg III: metatarsus 199–225, tarsus 122–126. Leg IV: trochanter 128–134 (148–163), femur 97–103 (122–134), patella 134–145 (179–192), tibia 173–192 (243–251), metatarsus 220–246 (257–289), tarsus 176–191 (186–218).

Deutonymph

Much as in adults except that vxg is absent; genital region with 2 pairs of acetabula.

Remarks

Piona puripalpis belongs to the *rotunda* species-group as defined by Smith (1976). It is known from northern and eastern Australia (Figure 52).

ACKNOWLEDGEMENTS

This work was supported by grants from the Australian Biological Resources Study. I wish to thank Rhonda Butcher, David Cook, Jenny Davis, Michael Gray (AM), John Hawking, Tim Kingston (QVM), Torbjorn Kronstedt (SMNH), Brian Timms and Elizabeth Turner (TM) for the loan or gift of specimens. The Australian National Parks and Wildlife Service, the Western Australian Department of Conservation and Land Management, and the Northern Territory Conservation Commission granted permission to collect water mites in areas under their control. Field work was kindly facilitated by many individuals and organisations, most notably the Tropical Ecosystems Research Centre, CSIRO, the Western Australian Department of Conservation and Land Management, John Blyth, Marianne McKaig and Alan Andersen.

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Manuscript received 9 December 1994; accepted 24 August 1995.

Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia

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Abstract – Two new species of *Liagoceradocus*, *L. subthalassicus* and *L. branchialis*, from anchialine habitats (hypogean waters of marine origin) are described from Barrow Island and North West Cape, Western Australia.

INTRODUCTION

It is becoming clear that the systematic boundary between amphipods inhabiting epicontinental waters and coastal marine waters in Australia is indistinct. Whilst there are many species in genera and families confined to or characteristic of inland fresh waters, there are also many species which, though found in Australian fresh waters, belong to genera or families of typically marine habit or which display many taxonomic features linking them with marine ancestors (see, for example Barnard and Williams 1995). The occurrence in Australia of undoubted marine forms in waters of essentially oceanic origin located inland but at no great distance from the coast is not therefore unexpected. The problem, however, is how best to treat them in revisions of the Australian amphipod fauna: as epicontinental species, or marine species *sensu stricto*? In the event it has been considered best to treat them separately and not to regard them as an integral part of the Australian inland aquatic amphipod fauna.

In recent collections from anchialine sites on Barrow Island (20°46'S, 115°24'E), and North West Cape (22°25'S, 113°46'E), Western Australia, we located specimens of the marine genus *Liagoceradocus*. Description of these specimens form the basis of this paper, and the new species described herein (*L. subthalassicus* and *L. branchialis*) are not regarded as members of the amphipod fauna of Australian inland waters. For this reason they are not included in our series of papers reviewing this fauna, but dealt with separately.

Methods of description follow those of Williams and Barnard (1988) except that L represents left and R, right. All specimens are lodged in the Western Australian Museum, Perth (WAM).

Genus *Liagoceradocus* Barnard

Liagoceradocus Barnard, 1965: 504.

Remarks

The genus *Liagoceradocus* Barnard, 1965 was erected for a pair of specimens taken from Ifaluk Atoll, Caroline Islands. Six species have so far been assigned to the genus, all from interstitial and subterranean marine waters of the tropical Pacific ocean. Rondé-Broekhuizen and Stock (1987) considered *Liagoceradocus* a viable genus distinct from *Hadzia*, whereas Stock and Iliffe (1991) considered it a doubtful genus because of the poor initial description of the type, and poor condition of the types. Stock and Iliffe (1991) questioned the assignation of other species to the genus on the grounds of the unique maxillipedal palp and distinct, spine-less palm of the second gnathopod of *Liagoceradocus pusillus* Barnard 1965. Barnard (1977), when assigning a second species to the genus, reduced the status of *Liagoceradocus* to a subgenus of *Hadzia*, although the genus was maintained by Barnard and Barnard (1983). Nevertheless, subsequent species have been attributed to *Liagoceradocus*. Stock and Iliffe (1991) themselves added a further two species despite the concerns expressed above. Furthermore, they noted that sexual dimorphism of the third pleopod was evident in some species while absent from others (although they suggested this may have been a reflection of lack of adult males among collections, whilst in some descriptions pleopods were not fully described). However, inconsistency of sexual dimorphism has not necessarily been regarded as contrary to generic compatibility. Williams and Barnard (1988) reported species of *Neoniphargus* may or may not display sexual

dimorphism in both the possession of antennal calceoli and of notched gnathopodal palms.

In this paper we accept *Liagoceradocus* as a valid genus and ascribe two new species to it: *L. subthalassicus* and *L. branchialis*. The presence of the genus in the Indian Ocean considerably extends its known area of distribution.

Liagoceradocus subthalassicus sp. nov.

Figures 1–3

Material Examined

Holotype

♀ 3.5mm. Unique (WAM 258-95, collection BES546).

Type locality

Ledge Cave B-1, an anchialine cave on Barrow Island, Western Australia, Australia (20°48'S, 115°20'E), collected by trapping, 28 July 1992, W.F. Humphreys and B. Vine.

Diagnosis

Pleonites naked except for 3 small dorsal setae on pleonite 4. *Head*. Rostrum weak, lateral cephalic lobes moderately projecting, antennal sinus small and distinct, eyes absent. *First antenna* elongate, longer than A2, ratio of peduncular articles 23:21:11, accessory flagellum 2 articulate, no calceoli. *Second antenna* short, flagellum much shorter than peduncle, calceoli absent. *Upper lip*. Apical margin rounded, symmetrical. *Mandible*. Palp 3 articulate, ratio of articles 17:39:41, article 1 not setose, article 2 bearing 4 strong medial setae, article 3 sub-falciform, almost linear, setate, approximately equal in length to article 2, setae = D9, E4. Accessory blades (rakers) = 9, without inter-raker plumose setae but 1 additional short naked seta proximally. No additional serrations beyond rakers. *Lower lip* bearing small vestigial inner lobes. *Maxillae* moderately setose medially. *First maxilla* inner plate triangular or semi-circular, linear medially, with 12 plumose medial setae, outer plate with 7 spines, palps asymmetric, both plates well covered in pubescence. *Second maxilla* inner plate with oblique facial row of long setae, baso-medial and outer-distal margins, and apical margin of the outer plate pubescent, both plates with moderate to strong apical setae. *Maxilliped*. Inner plate long, extending beyond M0.5 of the outer plate, laterally pubescent, with a distal row of 5 plumose setae, 3 blunt naked tooth spines, 1 sub-distal medial spine on the left side only, and 1 sub-marginal sub-distal medial spine forming a short row with 2 long plumose setae at M0.5 and M0.7. Outer plate broad with 5 naked and 2 plumose distal setae, 2 strong, short distal sub-marginal medial tooth spines, the

disto-medial margin carved into 2 or 3 acuminate sinuosities merging basally with a medial row of 8 slender spines which become sub-marginal distally leaving the sinuosities naked. Palp article 2 without lateral setae, article 3 with a single lateral seta at M0.9, and 2 pairs of latero-facial setae at M0.4 and M0.7, articles 2–3 moderately setose medially, article 3 bearing a transverse band of pubescence at M0.5, and distal comb rows of setae toward the base of the dactyl, the apex is moderately produced, dactyl unguiform with 3 distal accessory spinules, the nail of moderate length, bearing a single dorsal spinule of equal length. *Coxae*. C1–3 longer than broad, C4 as broad as long, C1–4 with few posterior spines, C1 not expanded below, C4 not excavate posteriorly. *Gnathopods* subchelate, 1–2 diverse. Setae of articles 4 ordinary, not rastellate. *First gnathopod* small, feeble, carpus longer than propodus, not lobate, merus not lobate but posteriorly bulbous and pubescent, left palm slightly oblique, right palm transverse, both short, palmar spines not symmetrically bifid but with small sub-apical trigger like extensions. Spines at corner of palm = 2 stout bifid medial and lateral, and 1 elongate, slender, lateral. Few spines or setae along the palm, dactyls lacking recumbent inner tooth spines, nail present. *Second gnathopod* enlarged, 2x G1, carpus equal to propodus, with long keel like pubescent posterior lobe, posterior setae sub-marginal proximally, to facial distally, hand ovate, palm oblique, moderately spinose and setulose, defining corner with 2 stout medial spines and 2 elongate lateral spine-setae, nail absent, free posterior margin bearing long 'hadziid' setae (Barnard and Barnard, 1983). *Pereopods* feeble, weak. P3–4 smaller, weaker than P5–7, posterior spine sets on article 6 of P3–4 weak, uneven. P5–7 moderately elongate, P7 longest, P5 shortest, article 2 moderately expanded, ovate, slightly lobate on P6, lobate on P7. Dactyls of P3–7 bearing 2 or more distal accessory spinules as well as an outer basal penicillate setule. *Gills*. Coxae 2–6 each with a single flask shaped gill. Gill 6 not reduced. *Oostegites*. Coxae 2–5 each bearing a thin, poorly setose oostegite.

Epimera. Posteroventral tooth of E1–3 absent except for a tiny spine on E3. Posterior margins smooth and naked except for 1 or 2 small setae. E2–3 with single, small posterior ventro-facial spinules and 1 or 2 antero-facial spines. *Pleopods* with dissimilar numbers of setae and retinacula. Rami extending sub-equally and symmetrically, baso-medial setae not bifid. *Urosome*. With 3 ventro-distal spines on urosomite 1 at the base of U1. *Uropods*. U3 extended, magniramous, dispariramous, peduncle short, outer ramus 2 articulate. Apico-lateral corner of peduncles of U1–2 with 1 spine, the dorsal margins spinose, medial margin of peduncle of U1 with 1 apical spine, of

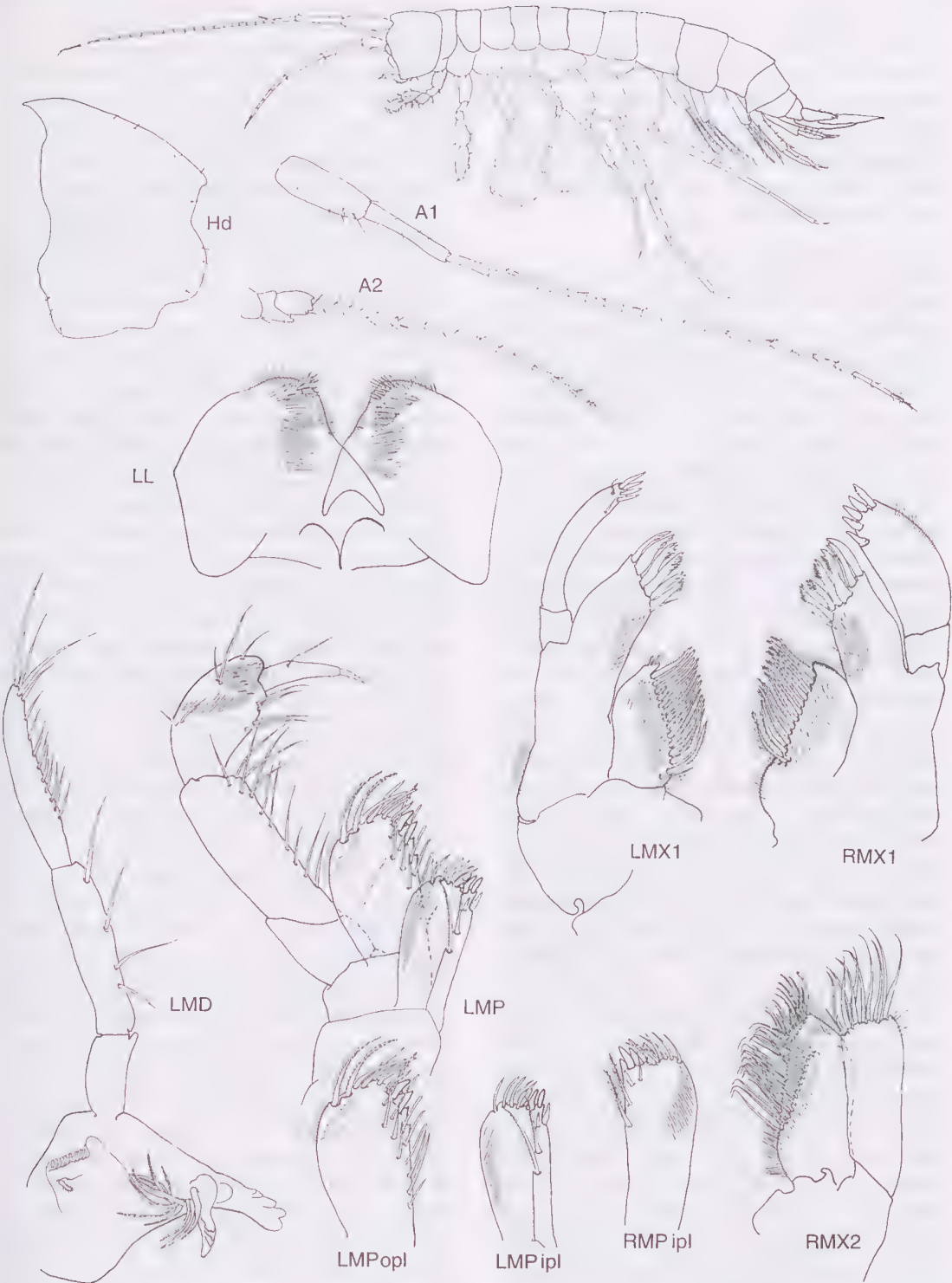


Figure 1 *Liagocera docus subthalassicus* sp. nov., holotype, female 3.5 mm. Whole animal, head, antennae and mouthparts.

U2 with 4. Rami sub-equal, the lateral being the shorter. Peduncle of U1 with baso-facial spine. Rami of U1-2 with single spine rows. Medial setae of outer ramus of U3 present as 3 distal pairs, sub-distal peduncular setae and spines absent, rather a pair of mid-distal spines at the base of the outer ramus. *Telson* longer than broad, cleft 100%, lobes moderately convex laterally, linear medially, with sub-apical setation, medial and lateral setal spines. Penicillate setules absent.

Description of holotype (female)

Body 3.5 mm. (Figure 1). Poorly armed dorsally. *Head*. Rostrum weak, lateral cephalic lobes moderately projecting, antennal sinus small, distinct, eyes absent. *First antenna* (Figure 1) length 0.75X body. Flagellum longer than peduncle - 1.8x (98:53) - peduncular article 1 longest, bearing a long strong medio-distal seta, article 3 shortest (ratio of lengths; 230:210:110), setae sparse, accessory flagellum 2 articulate, reaching M0.4 of article 2 of primary flagellum, 2nd article reduced - 4:11 of article 1. Primary flagellum of 23 articles, uniform, sparsely setulate, aesthetascs present on articles 6,7,9,15,18,21,22, calceoli absent. *Second antenna* (Figure 1) length 0.4x body, peduncle longer than flagellum (130:76), gland cone well developed and extending to M0.5 of the third article, peduncular article 3 with few setae or spines, articles 4-5 equally long, slender, moderately setulate. Flagellum 7 articulate, calceoli absent. *Upper lip* (Figure 1). Apical margin rounded, symmetrical, with short marginal pilia. *Lower lip* (Figure 1). Inner lobes small, basal. *Mandibles* (Figure 1). Similar, palp article 1 shorter than 2, articles 2-3 equal, article 3 with 9D and 4E setae, incisor 4 toothed, lacinia mobilis with 4 teeth, the fourth denticulate, 9 setose accessory blades, molar bearing a very short minutely setulate distal seta. *Maxillae* (Figure 1). Right and left palps of *first maxillae* asymmetric; 5 apical tooth spines on the right palp, 4 slender apical spines and 2 accessory sub-apical spines on the left. The outer plate bearing 6 denticulate apical spines and a single slender 7th medio-distal spine on the left, the right outer plate bearing 7 denticulate or barely denticulate apical spines and a single moderate, naked, medial, sub-apical spine. Inner plate with 12 (right) or 13 (left) medial plumose setae. *Second maxilla*, both plates with outer apical margin pubescent. Inner plate with baso-medial pubescence extending across the face basal and distal to an oblique row of setae forming a sub-apical pubescent crescent. The outer plate with few medial and several apico-medial setae. *Maxilliped* (Figure 1). Inner plate without ventro-facial spines. *First gnathopod* (Figure 2) coxal plate with short setae ventrally not extending beyond the posterior corner. Article 5 not lobate, propodus trapezoidal,

expanding slightly apically, longer than wide (78:52), the corner of the left palm marked with 1 lateral and 1 medial strong bifid spine and a single moderate lateral seta, the right palm marked laterally and medially with 2 strong spines and 1 long lateral seta. Palm slightly convex posteriorly, excavate anteriorly, with fine marginal cusps, left palm slightly oblique. Dactyl almost reaching the palmar corner, the right more slender than the left with 4 accessory spinules, sub-marginal on the lateral face, and a single dorsal spine at M0.2, the left with 3 facial spinules, and a 4th distal spine almost as an accessory tooth, and both lateral and medial sub-dorsal spines at M0.25 and 0.20. Left dactyl bearing distal nail, absent on right. *Second gnathopod* (Figure 2) dactyl without nail, bearing 3 inner accessory spines at M0.65-0.75, and a single small seta sub-marginal on the medial face at M0.4. Palm with 3 lateral and 3 medial stout trigger spines as well as 2 strong medial trigger spines and 2 long apically curved spines defining the palmar corner. Palmar length sub-equal to the free posterior length of the article. Free margin and corner of palm bearing long 'Hadziid' spines. Coxal plate broader than of G1, but still longer than broad, moderately setose both proximally and distally, otherwise naked. *Pereopods* (Figure 2). Coxae 3-4 with weak ventral setae, coxa 4 not excavate posteriorly, the posterior margin of article 6 of P3-4 armament formula S-S-S-S and S-S-S-Ss, P3-4 (89-80) smaller than P5-7 (98-115-170). Posterior margin of article 6 of P7 armament formula S-S-S-S-2S. Anterior spine sets of article 6, P7 not displaced by any keel like expansion. Coxae 5-7 bearing few setae on the ventral margin of the posterior lobes, article 2 moderately expanded bearing a small lobe on P6, moderate on P7, P7 bearing thin, short posterior setae. Dactyls of P3-7 bearing 2 or more distal accessory spinules; ie. 2 additional spinules as well as an outer basal penicillate setule. *Gills*. Coxae 2-6 each with a single flask-shaped gill. Gill 6 not reduced. *Oostegites* (Figure 2) of coxae 2-5 strap shaped, poorly setose. *Epimera* (Figure 3) 1-2 post-ventrally rounded, posteriorly convex, smooth, sparsely setulose. E1-3 with 0,1,2 ventro-facial spines. *Urosome* poorly armed dorsally. *Pleon*. Pleonite 1-6 with small dorsal setae in the formula 1-3-4-2-0-0. Dorso-lateral setae absent, pleonite 4 with 3 disto-ventral spines at the base of uropod 1. *Pleopods* (Figure 3). Retinacula 2 per pleopod, accessory retinacula variable; pleopod 1 with 2, pleopods 2-3 with 1. Basal articles of inner rami with paired, non-bifid setae, of outer rami, single setae. Rami extending sub-equally, outer with 10-11-10 articles, inner with 8-7-9 articles. *Uropods*. (Figure 3). *First uropod* peduncle length equal to length of inner ramus; medial margin bearing a row of 3 dorsal spines; mid-lateral row of 4 spines; single apico-

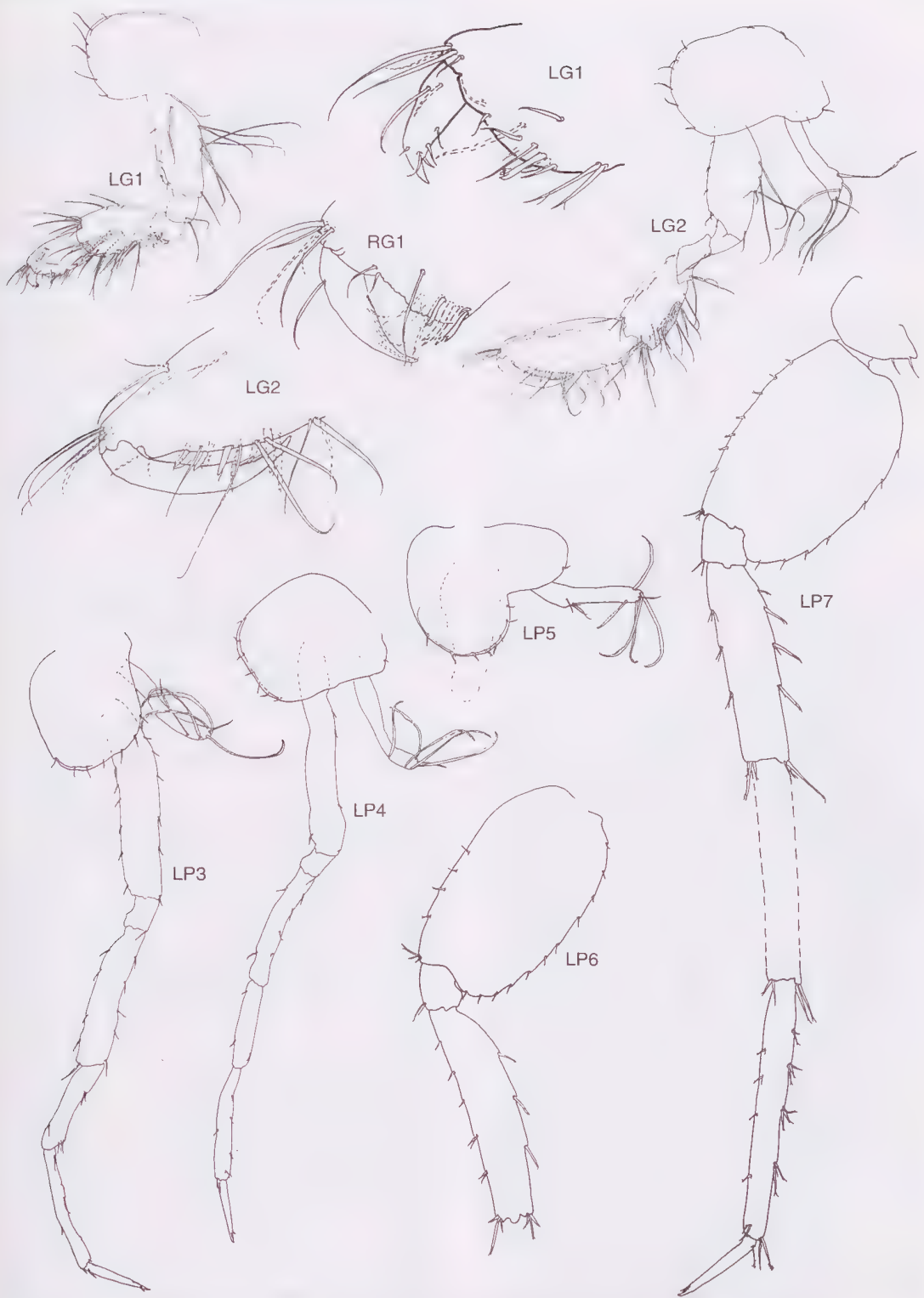


Figure 2 *Liagoceradocus subthalassicus* sp. nov., holotype, female 3.5 mm. Gnathopods and pereopods.

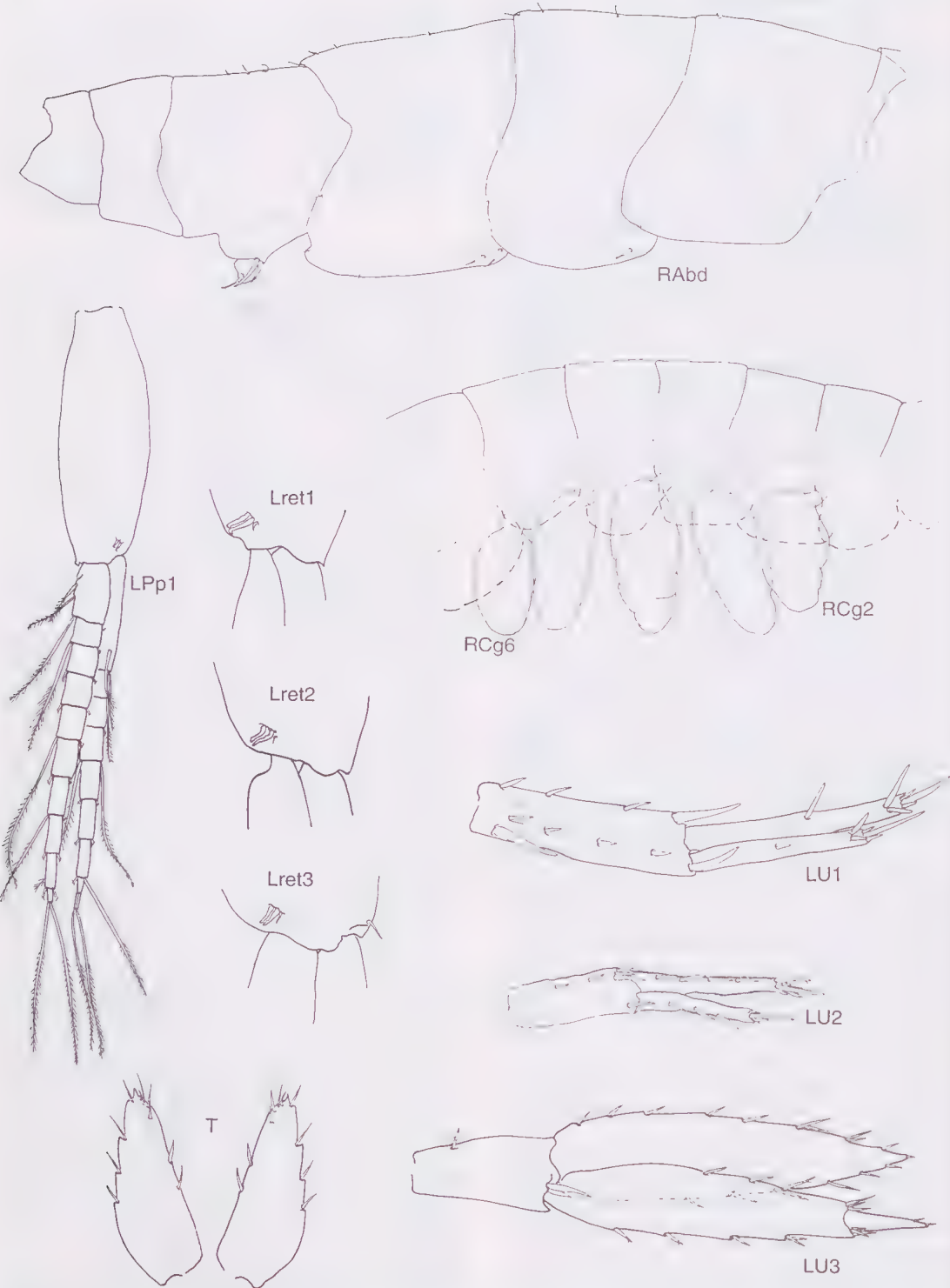


Figure 3 *Liagoceradocus subthalassicus* sp. nov., holotype, female 3.5 mm. Abdomen, gills, pleopods, uropods and telson.

lateral and apico-medial spines, prominent baso-facial spine. Rami unequal; inner ramus longer (90:75). Spine rows of rami reduced to a single dorsal spine on each, at M0.5, apices of rami each bearing 5 spines. *Second uropod* peduncle sub-equal in length to the shorter, outer ramus, bearing two dorso-medial spines at M0.4 and M0.7, a single dorsally displaced, sub-apical disto-lateral spine and 4 similarly arranged spines medially. Inner ramus longer than outer (77:58), outer ramus bearing a single row of 3 dorso-lateral spines and 4 terminal spines, inner ramus with a row of 4 dorso-medial spines and 5 terminal spines. Medial margin of peduncle and both margins of rami bearing small tooth spines. *Third uropod* magniramous, dispariramous. Peduncle short (60:160), with a single baso-medial seta at M0.3 and a pair of apico-dorsal spines. Outer ramus of 2 articles, proximal article bearing lateral and disto-medial marginal spines and clusters of 3 apical spines both laterally and medially; distal article shorter (35:125) with 2 medio-distal setae only. Inner ramus of one article, lanceolate, sub-equal in length to outer ramus, marginal spines evenly spaced, discontinuous basally on the lateral margin. *Telson* (Figure 3) 2.3x as long as wide, 2x urosomite 3, cleft 100%. Apices a rounded point, sub-apices notched bearing single medial and lateral short spines and 3 medial sub-marginal spines, 3 lateral and 2 medial spines marginal on each lobe. Penicillate setules absent.

Distribution

Barrow Island, Western Australia.

Relationship

Liagoceradocus subthalassicus shows some minor variation from the genus as originally described by Barnard (1965), but not from the generic characteristics of species assigned to the genus later or by Barnard and Barnard (1983). *L. subthalassicus* differs in the presence of rudimentary inner lobes of the lower lip, of palmar spines on the second gnathopod, and in having a greater number of D setae on the mandibular palp.

The new species differs from *L. pusillus* Barnard in the absence of 2 dorsal spines on urosomites 1–2, although pleonite 4 bears 3 small setae, in the presence of a very weak rostrum, larger lateral cephalic lobes, palmar spines on the second gnathopod, a shorter article 1 on the mandibular palp and an extra seta on the second article and 9 rather than 6 D setae of the third article, a degenerate molar seta, presence of small basal lobes to the lower lip, pubescence on the inner face of the inner plate of the second maxilliped, relatively larger and longer fifth article with a keel-like posterior lobe on the second gnathopod, moderate expansion of the second article of

pereopods 5–7 (on P6 this article is post-ventrally lobate), and the telson lacks penicillate setules.

Liagoceradocus subthalassicus differs from *L. lonomaka* Barnard, 1977 in possessing a slightly oblique left palm on the first gnathopod, palmar spines on the second gnathopod, a shorter first antenna, extremely short molar seta, 9 rather than 7 or 8 D setae on the third article of the mandibular palp, more slender third article of the maxillipedal palp which is also less spinous although facially pubescent with distal comb rows of setae, small basal inner lobes of the lower lip, and the third uropod more nearly magniramous.

Liagoceradocus lobiferus Stock and Iliffe, 1991 is similar to *L. lonomaka* except for an apically bulbous third article of the maxillipedal palp, more elongate and less lobate second article of the seventh pereopod. *L. unciferus* Stock and Iliffe, 1991 is similar to *L. lobiferus* except in the form of the gland cone of the third article of the second antenna, almost symmetrical palps of the first maxilla, lack of spines on the first urosomite, and the morphology of the male endopodite of the third pleopod. *L. subthalassicus* thus differs from *L. unciferus* in the form of the gland cone, being similar to *L. lobiferus*, and the asymmetry of the palps of the first maxilla, and from *L. lobiferus* in lacking spines on the first urosomite, having a shorter third article, longer accessory flagellum and greater number of aesthetascs – although of shorter length – on the first antenna. There is a rudimentary molar seta, the mandibular palp third article is longer and bears an extra E seta, the inner lobe of the first maxilla is more slender and triangular, bearing 13 L, 12 R plumose setae, the outer lobe with 6 L and 7 R denticulate distal spines and 1 small naked medio-distal spine on each, the palps bearing on the left 4 slender distal and 2 short sub-distal spines, on the right 4 + 1 robust spines. The outer lobe of the second maxilla bears many long distal setae, not, however, arranged in two discrete rows as in *L. lobiferus*, the inner lobe bears an oblique row of 14 setae, the maxillipedal palp article 3 is more slender, the dactyl more setate, the outer lobe of the maxilliped bearing two disto-medially placed, rather than five robust, medial spines, the medial margin is carved into acuminate sinuosities proximally, the left inner lobe with three distal, one sub-distal and one small sub-distal sub-marginal spines the right inner lobe with three distal and one sub-distal spines. The first gnathopod bears posteriorly on the second article six long apically curved setae and a single long straight seta, the same article of the second gnathopod with three long curved and two short setae borne on a small mid-marginal posterior keel like extension, the fifth article is lobate the lobe elongate and keel like, the setae of propodus being more marginal than in *L. lobiferus*, the palmar

corner is marked additionally by another two 'hadziid' setae, the palm and dactyl are more spinous, the dactyl lacking recumbent inner teeth. The oostegites bear more distal setae, urosomite one has three rather than two ventro-distal spines at the base of the first uropod, the peduncles of the first uropod are less spinous, the second article of the third uropod and telsonic lobes are more slender, the telson lacks penicillate setules.

Liagoceradocus subthalassicus is similar to *L. dentiferus* Ledoyer, 1982 in that the third article of the maxilliped is curved and the length less than twice the width, second and third coxal plates are longer than wide, and the palm of the second gnathopod bears both setae and spines. *L. subthalassicus* differs from *L. dentiferus* in the absence of proximal spines on the medial margins of the telsonic lobes, such spines being located in the distal half of the margin, the width of the fourth coxa is as great as the length, and the second article of pereopods 5 to 7 is post-ventrally lobate.

Liagoceradocus subthalassicus differs from *L. acutus* Andres, 1978 in the greater relative length of the third article of the peduncle of the first antenna, shorter flagellum with fewer articles and aesthetascs on both antennae, rudimentary inner lobes to the lower lip, on the mandible an extremely short molar seta, simple right lacinia mobilis, fewer setate accessory spines, short first article of the palp which bears an extra E seta on the third article, fewer denticulate spines on the outer lobe of the first maxilla which bears asymmetrical palps, fewer more robust setae in the oblique facial row of the second maxilla, the inner lobe of the maxilliped without a sub-distal oblique row of setae rather with a sparse sub-marginal facial row. The coxa and second article of the first gnathopod have fewer spines and setules, the palmar angle distinct on the right side only although marked by fewer spines, the palm is without spinules and with few setae. The coxa and second article of the second gnathopod are less armed, the lobe of article five is keel like, the palm bears two lateral and two medial spines, the palmar margin (of the female) is equal to the free posterior margin, coxae of pereopods 3 and 4 are equal, coxa four bearing a small posterior seta, article two of P5 is more expanded and ovate, and there are few armaments on any article. Pereopod 6, article one is equal to that of P5. Coxal gills 3-4 are largest, gill 6 smallest. The epimera are without an oblique ridge and bear few spines; E2-3 with 1-2 antero-sub-marginal spines, and the posterior corners of each is rounded rather than acuminate. The pleopods are without bifid spines. The first urosomite bears three ventro-distal spines at the base of the first uropod, the peduncle of the second uropod bears two apico-medial spines and a disto-medial group of four small spines, the outer ramus

has three dorso-facial rather than two medio-distal spines, the apex of the third uropod an additional sub-apical setule. The telson is lanceolate rather than ovate, bearing one rather than two disto-lateral spines and is without penicillate setules.

L. subthalassicus differs from *L. branchialis* in: the absence of a distinct posterior lobe on the carpus of the second gnathopod; reduced rather than moderate molar seta; a greater number of medial setae on the second and third articles of the mandibular palp; longitudinal rather than oblique row of medial plumose setae on the inner plate of the first maxilla; greater pubescence of the maxillae; denticulate rather than spinous apical setae on the L outer plate of maxilla 1; absence of a small post-ventral lobe on the second article of P5; three ventro-distal spines rather than a small, single seta on urosomite 1 at the base of U1; presence of accessory retinacula on pleopods 1-3; greater setation of U1-3; presence of lateral setation, but absence of penicillate setules on the telson which is not tumid laterally.

Etymology

Named for the nature of the type locality.

Liagoceradocus branchialis sp. nov

Figures 4-6

Material Examined

Holotype

♂ 'a' from sample BES 4282, body length 4.0 mm, Cave C-28, Cape Range peninsula, Western Australia, Australia (22°25'S, 113°46'E), 26 May 1995, in saline water, A.A. Poole, D. Warren (WAM 257-95).

Paratypes

1 ♂ 'b' from sample BES 4282, body length 3.5 mm, same data as holotype (WAM 272-95); 3 ♂ same data as holotype except 24 May 1995, body length 3-5 mm (WAM 273-95 to 275-95); 1 ♂, same data as holotype except 25 May 1995, body length 3.5 mm (WAM 256-95).

Type locality

Bundera Cenote, (C-28) below pycnocline in a tidal, almost anoxic, anchialine cave (22°25'S, 113°46'E) on North West Cape, Western Australia.

Diagnosis

Pereonites and *pleonites* bearing few fine dorsal and dorso-lateral setae, without carinations or teeth. *Head*. Rostrum weak, lateral cephalic lobes weakly projecting, antennal sinus small and distinct, eyes absent. *First antenna* elongate, longer than A2, ratio of peduncular articles 24:27:10,

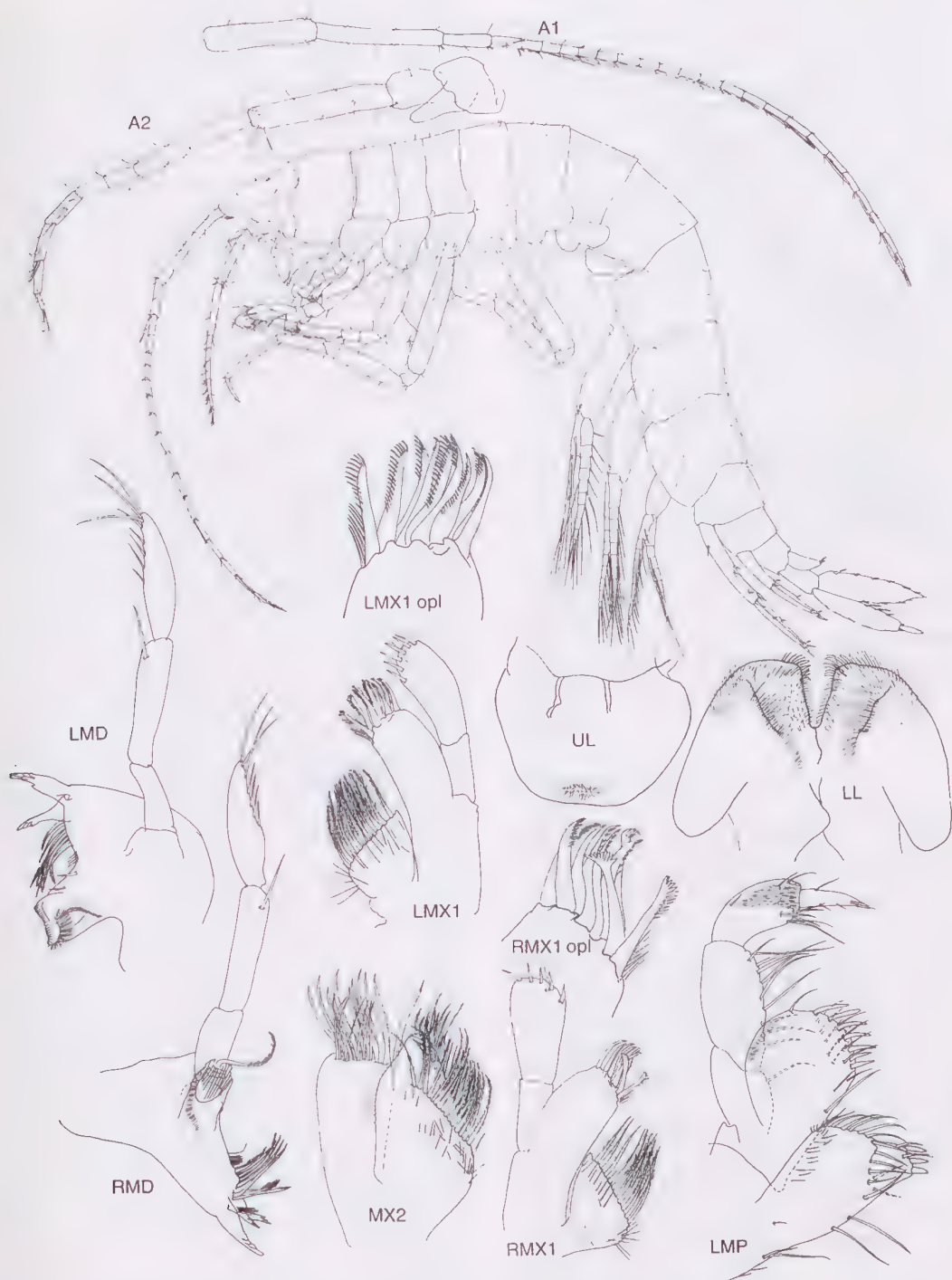


Figure 4 *Liagoceradocus branchialis* sp. nov., holotype, male 4.0 mm. Whole animal (male 'c' 3.5 mm), antennae and mouthparts.

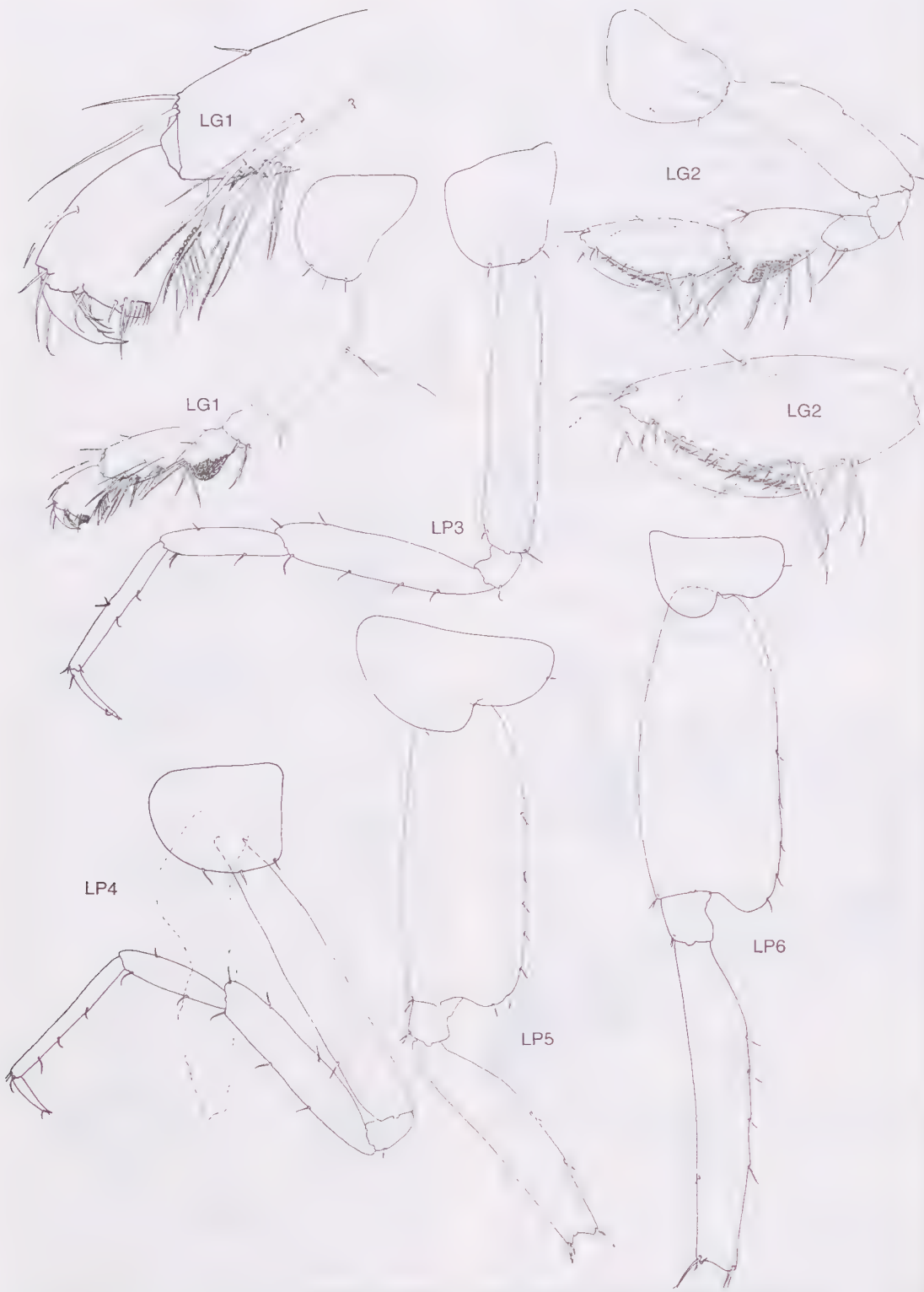


Figure 5 *Liagoceradocus branchialis* sp. nov., holotype, male 4.0 mm. Gnathopods and pereopods.

accessory flagellum 2 articulate, without calceoli. *Second antenna* short, flagellum much shorter than peduncle, calceoli absent. *Upper lip*. Apical margin rounded, symmetrical. *Mandible*. Palp 3 articulate, ratio of articles 1:2:2, article 1 not setose, article 2 bearing 1 strong medial seta, article 3 sub-falciform, setate, sub-equal in length to article 2, setae = D5, E3. Accessory blades (rakers) = 8L, 7R, with few inter-raker plumose setae and few additional setae leading to the base of the molar. *Lower lip* with rudimentary inner lobes. *Maxillae* sparsely setose medially. *First maxilla* inner plate triangular, the distal end linear, acute, bearing 10 plumose setae, outer plate with 9L spinous setae and 7R denticulate and spinous setae, palps asymmetric, inner plate sparsely pubescent. *Second maxilla* inner plate with oblique facial row of plumose setae, outer plate without pubescence, both plates with moderate and strong apical setae. *Maxilliped*. Inner plate long, extending beyond M0.5 of the outer plate, bearing sparse lateral pubescence, distally narrowed, and bearing three naked tooth spines and two moderately elongate naked setae, laterally and facially a row of long setae, and medially and baso-medially sparse setae. Outer plate broad, ovate with 7 curved naked apical and disto-medial spines without plumose distal setae, bearing submarginal, facial and ventro-facial slender setae. Palp article 2 without lateral setae, article 3 with a single sub-marginal lateral seta at M0.4, and 2 latero-facial setae at M0.8 and M0.9, article 2 moderately setose medially, article 3 bearing disto-facial pubescence, and a few elongate disto-medial setae basal to the dactyl, the apex not produced, dactyl unguiform with 2 distal accessory spinules, equal to the nail which is of moderate length, and bearing two accessory posterior spinules. *Coxae*. C1–2 longer than broad, C3–4 as broad as long, C1–4 without posterior spines, C1 not expanded below, C4 not excavate posteriorly. *Gnathopods* subchelate, 1–2 diverse. Setae of articles 4 ordinary, not rastellate. *First gnathopod* small, feeble, carpus longer than propodus, not lobate, merus lobate the lobe pubescent, palms transverse, palmar spines symmetrical, not bifid, without small sub-apical trigger like extensions. Spines at corner of palm absent, rather with an adjacent row of 7 slender setae. Few spines or setae along the palm, dactyls lacking recumbent inner tooth spines, but bearing 2 posterior accessory spines, and a pair of elongate setae arising adjacent the base. Dactylar nail present. *Second gnathopod* enlarged, 1.4x G1, carpus equal to propodus, with shallow, pubescent posterior lobe, posterior setae sub-marginal proximally, to facial distally, propodus ovate, palm oblique, moderately spinose, defining corner with 2 elongate 'hadziid' setae, 1 moderate medial seta and single lateral and medial bifid setae, posterior

margin bearing few long 'hadziid' setae (Barnard & Barnard, 1983). Dactyl bearing several recumbent inner tooth spines, nail absent. *Pereopods* slender, weak. P3–4 smaller, weaker than P5–(7), posterior spine sets on article 6 of P3–4 sparse, weak. P5–(7) moderately elongate, (P7 longest), P5 shortest, article 2 moderately expanded, ovate, slightly lobate on P5–6. Dactyls of P3–4 bearing 2 distal accessory spinules as well as an outer basal penicillate setule. *Gills*. Coxae 2–6 each with a large flask shaped gill. Gills 4–5 largest.

Epimera. Posteroventral tooth of E1–3 absent. Posterior margins smooth and naked except E2–3 with single, small posterior setae, E3 bearing a single, small antero-ventral seta. *Pleopods* similar each with 2 retinacula, without peduncular setae, and all plumose setae of rami simple. Rami extending sub-equally and symmetrically. *Urosome*. With a single, tiny ventro-distal spine on urosomite 1 at the base of U1. *Uropods*. U3 extended, magniramous, dispariramous, peduncle short, outer ramus 2 articulate. Apico-lateral and apico-medial corners of peduncles of U1–2 with 1 spine, the dorsal margins of U1 spinose, peduncle of U1 bearing a baso-facial spine. Rami sub-equal, the lateral being the shorter, rami of U1–2 with single spine rows, the medial margins of rami bearing fine setae. Rami of U3 bearing medial, lateral and apical setae. *Telson* shorter than broad, cleft 100%, lobes moderately tumid laterally, and medially, with sub-apical setation, medial and lateral setae virtually absent. Penicillate setules present sub-apically.

Description of holotype (male)

Body 4.0 mm. (Figure 4). Poorly armed dorsally. *Head*. Rostrum weak, lateral cephalic lobes weakly projecting, antennal sinus small, distinct, eyes absent. *First antenna* (Figure 4) length 0.6x body. Flagellum longer than peduncle – 1.9x (115:61) – peduncular article 1 shorter than article 2, bearing weak setae only, article 3 shortest (ratio of lengths; 24:27:10), with sparse setae, accessory flagellum 2 articulate, reaching M0.7 of article 1 of primary flagellum. Primary flagellum of 23 articles, article 1 elongate, 1.8x article 2, articles 2 to penultimate article progressively elongate and slender, most bearing aesthetascs, sparsely setulate, calceoli absent. *Second antenna* (Figure 4) length 0.2x body, peduncle longer than flagellum (65:35), gland cone well developed and extending to M0.7 of the third article, peduncular article 3 with few setae or spines, article 4 longer than article 5, both slender, moderately setulate. Flagellum 6 articulate, calceoli absent. *Upper lip* (Figure 4). Apical margin rounded, symmetrical, with a small terminal area of short pilia. *Lower lip* (Figure 4). Inner lobes small, rudimentary, indistinct. *Mandibles* (Figure 4). Asymmetric. Left mandible: palp article 1 shorter

than 2, articles 2–3 equal, article 2 bearing a single, strong moderately long medial seta at M0.8, article 3 with 5D and 3E setae, incisor 5 toothed, lacinia mobilis with 4 teeth, 8 setose accessory blades, 4 short and 2 moderately stout setae leading to the molar, molar tritulative, with fine marginal setae, and bearing a pappose distal seta. Right mandible palp article 3 bearing 4D and 3E setae, incisor 4 toothed, lacinia mobilis bifid, both articles denticulate, and bearing small, fine mid basal setae, 7 accessory blades and 1 interraker plumose seta, few additional fine setae lying between rakers and molar, molar similar to left mandible. *Maxillae* (Figure 4). Right and left *first maxillae* asymmetric; left palp with 6 facial, sub-terminal, stout setae and 1 on the ventral face, left outer plate bearing 9 stout setae armed with marginal spines, right palp bearing 5 slightly shorter terminal setae and 1 ventral seta, the right outer plate bearing 9 stout setae, some with marginal spines others strongly dentate, or with a mix of spines and denticles, the outer plate of both bearing an apico-medial cluster of fine setae basal to the first and second terminal spines. Inner plate with 10 distal plumose setae on both sides. *Second maxilla*: inner plate bearing sparse facial and lateral pubescence, outer plate naked. Pubescence of inner plate extending across the face basal to an oblique row of 15 plumose setae, medial margin slightly oblique bearing a medial marginal row of 7 slender naked setae, a distal sub-marginal row of plumose setae, and distal marginal row of mixed plumose setae and 2 stout rastellate setae. The outer plate without medial or lateral setae and apically a sub-marginal row of 7 slender naked setae and 10 long, stout rastellate setae. *Maxilliped* (Figure 1), Inner plate bearing few ventro-facial spines. *First gnathopod* (Figure 5) coxal plate with 2 short setae ventrally. Article 5 (carpus) not lobate, bearing strong posterior naked and rastellate setae. Propodus trapezoidal, expanding slightly apically, longer than wide (70:50), posterior margin bearing a row of 6 slender setae, the corner of the palm without lateral or medial spines, but a sub-distal row of 7 moderate, slender setae. Palm transverse, slightly convex posteriorly, with few adjacent setae, without marginal spination, or anterior excavation or marginal cusps. Dactyl reaching the palmar corner without recumbent inner tooth spines, but bearing 2 accessory spinules and a nail. *Second gnathopod* (Figure 5): larger than G1, the carpus posteriorly lobate and pubescent, bearing long, strong, apically curved setae, propodus ovate, palm strongly acute, dactyl extending beyond the corner defined by 2 long 'hadziid' setae and a slender seta laterally, and single lateral and medial bifid setae, palm bearing few short, simple setae, dactyl without a nail, bearing 7 recumbent, inner tooth spines and 5 sub-marginal, posterior,

accessory setae as well as a single small seta on the medial face at M0.6. Two moderate length spines arise from the propodus at the base of the dactyl. Coxal plate similar to G1, bearing 1 ventral, 1 antero-ventral, and 1 antero-facial setae. *Pereopods* (Figure 5). Coxae 3–4 each with 3 ventral setae, no posterior setae, coxa 4 not excavate posteriorly, the posterior margins of article 6 of P3–4 with few armaments; formulae S-S and S-S-S, P3–4 subequal, smaller than P5–(7). Coxa 5 bearing 1 antero-ventral seta, and coxae 5–7 bearing single setae on their posterior margins, article 2 moderately expanded bearing a small lobe on P5–6. Dactyls of P3–4 long and slender, bearing 2 distal accessory spinules; ie. 2 additional spinules as well as an outer basal penicillate setule. *Gills* of coxae 2–6 each with a large, single, flask shaped gill. Gill 5–6 largest. *Epimera* (Figure 6) 1–3 without posterior tooth, posteriorly convex to straight, smooth, without facial setae. E3 bearing a single antero-ventral seta, E1–2 each with a single posterior seta. *Urosome* poorly armed dorsally. *Pleon*. Pleonites 1–6 with few small dorsal setae, dorso-lateral setae largely absent, pleonite 4 with a single, small disto-ventral spine at the base of uropod 1. *Pleopods* (Figure 3): similar, retinacula 2 per pleopod, without accessory retinacula, peduncles without setae, rami extending sub-equally, without bifid or 'diamond head' setae; all setae similar, plumose. *Uropods*. (Figure 3). *First uropod* peduncle length greater than length of inner ramus; medial and lateral margins each bearing 2 setae, single apico-lateral and apico-medial spines, and a moderate baso-facial spine. Rami unequal; inner ramus longer (50:46), lateral ramus without setae except an apical group of 5, the medial ramus bearing a single medial seta and an apical group of 5 setae, the medial margins of both rami bearing a row of fine pubescence. *Second uropod* peduncle sub-equal in length to the shorter, outer ramus, without setae except for single lateral and medial apical setae. Inner ramus longer than outer (41:35), outer ramus bearing a lateral row of 2 setae at M0.6 and M0.7, and 4 terminal spines, the inner ramus with a single dorso-medial spine, and 5 terminal spines. Medial margins of both rami bearing small, pubescent setae. *Third uropod* magniramous, dispariramous. Peduncle much shorter than outer ramus (30:87), with a single small baso-medial seta, without any apical setae. Outer ramus of 2 articles, proximal article bearing 5 lateral, 2 plumose and 1 naked disto-medial marginal setae, and 1 and 2 apical spines respectively. The distal article short (18:70), with single, tiny medio-distal and apical setules. Inner ramus of one article, lanceolate, shorter than the outer ramus (80:87), marginal setae discontinuous basally on the lateral margin, 3 lateral and 6 medial setae, the baso-medial seta more robust, and a single tiny sub-apical, slightly

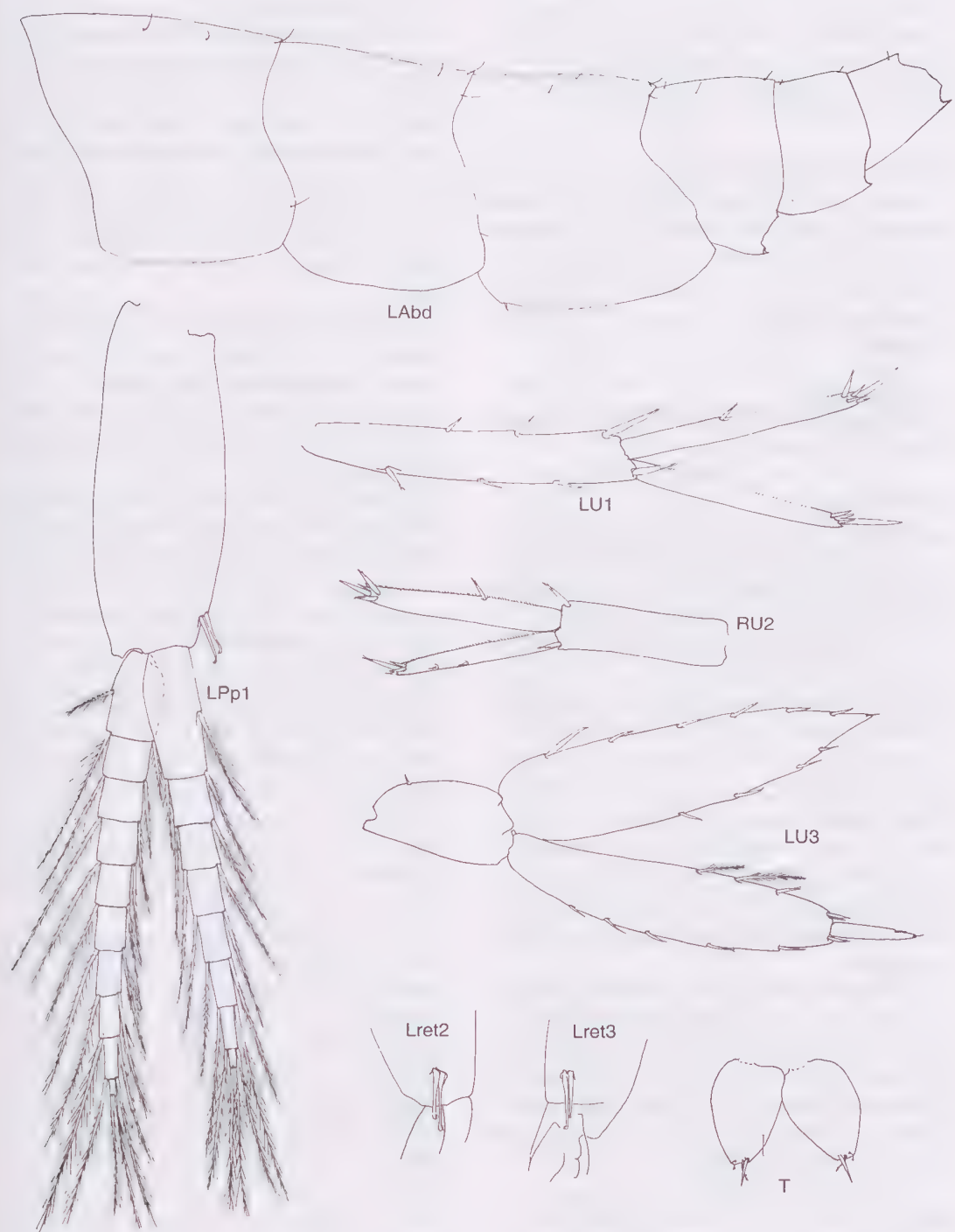


Figure 6 *Liagoceradocus branchialis* sp. nov., holotype, male 4.0 mm. Abdomen, pleopods and uropods.

medial setule. *Telson* (Figure 3) shorter than broad (45:63), sub-equal in length to urosomite 3, cleft 100%, laterally tumid, the apices rounded or slightly notched, bearing a moderately long single naked seta and 2 small penicillate setules, and on the left lobe a single sub-marginal medial seta at M0.7. Lateral penicillate setules absent.

Description of other material

Male 'c', 3.5 mm. A1 flagellum of 16 articles, aesthetascs present on articles 11, 14, 16; relative lengths of peduncular articles; 19:21:6 (compares with 24:27:10, converts to 24:27:8), length of flagellum relative to peduncle; 77:46 (compares with 115:61, converts to 115:68), and accessory flagellum reaching to end of article 1 of primary flagellum.

Distribution

Bundera Cenote (22°25'S, 113°46'E), North West Cape, Western Australia.

Relationship

Liagoceradocus branchialis, like other species assigned to the genus, differs from Barnard's (1965) original definition in minor ways. Rudimentary inner lobes are present on the lower lip, palmar setae are found on the second gnathopod, and there are 5 rather than 6 D setae on the third article of the mandibular palp, and which article is not longer than article 2. In keeping with the original definition of the genus the telson is deeply cleft, although, unlike in Barnard's revised (1977) concept, lateral setae (spines) are absent. *L. branchialis* differs also from *L. pusillus* Barnard in that the apex of the third maxillipedal palp article is not apically produced, the rostrum is reduced, but not entirely absent; the third epimeron is not acuminate; there are no dorsal spines on urosomites 1–2; sparse setae on the inner face of the inner plate of the second maxilla; post-ventral lobes on the second article of the fifth and sixth pereopods.

L. branchialis differs from *L. lonomaka* Barnard in the presence of a small rostrum; relatively shorter antennae; symmetric molarial setae; the third article of the maxillipedal palp is similarly armed but not as broad; the uropods are less setate, the peduncular spines of U2 are simple not forming a comb; the telson is without medial and lateral spines; the cuticle smooth, with few setae; the second article of P5 is broader than on P4.

L. branchialis differs from *L. acutus* Andres in the length of the A1 accessory flagellum which is relatively shorter; A2 is composed of peduncle and 6 rather than 14 flagellar articles, the gland cone is less tapered; the upper lip has less apical setation; mandibular palp article 3 has fewer D setae; the

inner lobe of the first maxilliped has fewer plumose setae; maxillipedal palp article 3 is not produced apically, and spines of the plates are naked, not setulate or rastellate; coxal plates bear fewer setae; G1 is without palmar corner spines, the palmar margin is without spinules or bifid spines; the legs are less setose or spinous; epimera are without an oblique ridge, the post ventral corners without teeth or acumination, ventral margins are without spines or setae; peduncles of pleopods bear 2 retinacula each without accessories, setae are all simple and plumose; basofacial spine of U1 is weak; peduncles and rami of uropods with fewer spines and setae; the telson is without lateral spines.

L. branchialis differs from *L. dentiferus* Ledoyer in that the second article of P5 is weakly lobate; the width of C4 is less than its depth; the palm of the second gnathopod has fewer spines or setae; telsonic lobes are without lateral or medial spines. The two are similar in that the third article of the maxillipedal palp is curved, and the dactyl bears accessory spinules.

L. branchialis differs from *L. unciferus* Stock and Iliffe in possessing a shorter A1 accessory flagellum, aesthetascs longer than flagellar segments; the gland cone of A2 is less pointed; fewer setae on articles 2–3 of the mandibular palp; less apical setae on the palp of the first maxilla; the G1 is without spines at the palmar corner, and without bifid spines; G2 dactyl bears larger recumbent inner tooth spines, there are fewer palmar spines, the palmar corner bears bifid rather than naked spines, as well as long 'hadziid' setae; coxae and Pereopods bear fewer marginal setae, coxa 4 is wider than long; epimeral plates 1–2 are post-ventrally rounded rather than pointed, without ventral setae or spines; pleopods are unmodified, similar, without bifid setae or accessory retinacula; uropods are less spinous; telson is without medial or lateral spines, with apical penicillate setules.

L. branchialis differs from *L. lobiferus* Stock and Iliffe; the body is similarly armed except for the absence of dorsolateral spines on urosomites 1–2; appendages are less spinous or setate; U3 is relatively longer; A1 peduncle article 2 is longer than article 1, the accessory flagellum is shorter than the first article of the primary flagellum, the primary flagellum has more articles but the same relative length, the aesthetascs are longer; A2 gland cone is broader and less pointed apically, the flagellum of similar numbers of articles; mandibular molar well developed, palps with fewer setae; first maxilla inner lobe with more plumose setae although similarly arranged, the processes of the spines of the outer plate are similar, the palps with fewer terminal spines; second maxilla bearing more setae both plumose

and rastellate; maxilliped article 3 not apically extended, the outer lobe ovate, not subquadrate, bearing 7 slender curved spines rather than 5 robust spines, the inner lobe pyriform with lateral, facial, medial setae and spines; propodus of G1 lacking spines at palmar corner and without bifid spines; palmar spines of G2 without triggers, dactyl bearing prominent recumbent inner tooth spines; coxal gills 4–5 largest, 1.5X gills of C1–2; pleopods simple without accessory retinacula, all setae plumose, not bifid; uropods with fewer setae and spines; telson without medial and lateral spines, with apical penicillate setules.

Etymology

Named for the presence of large coxal gills.

ACKNOWLEDGEMENTS

We thank the collectors of the material, Dr W.F. Humphreys and his assistants at the Western Australian Museum, and the Western Australian Museum for permission to examine the specimens. The Australian Biological Resources Study provided financial support. W.F. Humphreys received logistic support and victualling from West Australian Petroleum, Pty Ltd.

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Manuscript received 29 June 1995; accepted 9 October 1995.

A new genus of centipede, *Australoschendyla* (Chilopoda: Geophilomorpha: Schendylidae), from Western Australia

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Abstract – A new centipede genus *Australoschendyla* and two new species, *A. capensis* and *A. albanensis*, (Chilopoda: Geophilomorpha), are described from the Exmouth and Albany areas in Western Australia.

INTRODUCTION

Geophilomorph centipedes in the family Schendylidae are characterised by their mandibles having both a dentate and a pectinate lamina. Until now the only schendylid centipede known from Australia was the introduced European species *Schendyla nemorensis* (C.L. Koch 1837), found in Tasmania. (R. Mesibov, pers. comm). In the collections of the Western Australian Museum are several very small geophilomorphs of one species collected in Cape Range near Exmouth and of another species from the Bluff near Albany. They are clearly schendylids from the structure of the mandibles.

Schendylid taxonomy is complicated by the fact that it relies on factors to distinguish between genera that are not necessarily distinctive only of those genera. The two new Western Australian species are clearly closely related yet they do not key out to an existing genus in any guides (Attems 1929, 1947; Chamberlin 1947; Crabill 1961).

The Western Australian specimens have both one and two coxal pores per coxa in the same genus whereas the keys differentiate between either one or two as the sole number for a genus. The genus *Schendylurus*, from Africa and South America, is similar in some respects but *Schendylurus* species all have two coxal pores per coxa and lack the well developed claws on the last legs that the new species have (Brolemann and Ribaut 1912). For discussions about whether the presence or absence of features like claws on the last legs is in fact a valid generic one and a discussion of some other schendylid taxonomic matters, see Hoffman and Pereira (1991), Pereira and Hoffman (1993, 1995).

The two new species are very similar and rather than choose an existing genus and redefine it to include them, I have placed them in the new genus, *Australoschendyla*.

All specimens are lodged in the Western Australian Museum, Perth (WAM).

SYSTEMATICS

Family Schendylidae

Australoschendyla gen. nov.

Type species

Australoschendyla capensis sp. nov.

Diagnosis

Very small schendylid centipedes with one or two coxal pores per coxa. Second maxillary telopodites with claws with spines on the dorsomedial edge. Last legs with claws.

Description

Very small centipedes, white to yellowish white in alcohol, with a trace of yellowish brown on the forcipular segment. Labrum consists of sidepieces with several pointed fimbriae, midpiece an arch of blunt teeth. First maxillae with lateral palpi and articulated telopodites. Anterior border of the second maxillary coxosternite concave with no notch. Secondary maxillary telopodites with well developed apical claws which have spines on the dorsomedial edge (Figures 9, 12). Mandible of typical schendylid form with both pectinate and dentate laminae. Lamina basalis visible (Figures 2, 10). Forcipular coxosternite without chitinalines (pleurograms), the anterior border concave. The poison-claws have a number of incisures giving them a distinctly crenulate appearance. Poison calyx situated in the tibia/tarsus. Sternal pore-groups are present. Claws of all legs except the last pair with a ventral spiniform spur (Figures 7, 13). Telopodites of the last legs with apical claws. Anal pores absent.

Australoschendyla capensis sp. nov.

Figures 1–11

Material Examined

Holotype

♀, Cape Peninsula, site TL–6, Western Australia,

Australia, 22°10'S, 113°59'E, pitfall traps, 18 May–4 June 1990, J.M. Waldock (WAM 92/1318).

Paratypes

Australia: Western Australia: 1 ♂, Cape Peninsula, site TL-12, 22°10'S, 113°59'E, pitfall traps, 22 May–4 June 1990, J.M. Waldock (WAM 92/1322); 2 ♀, 1 ♂, same data as holotype (WAM 92/1317, 92/1319–20); 1 ♂, Cape Peninsula, gorge near cave C.256, 22°01'S, 114°03'E, 27 May 1990, J. Waldock (WAM 92/1315); 1 ♂, Cape Peninsula, near cave C.254, *Eucalyptus* sp. leaf litter, 22°02'S, 114°02'E, 30 May 1990, J.M. Waldock (WAM 92/1316).

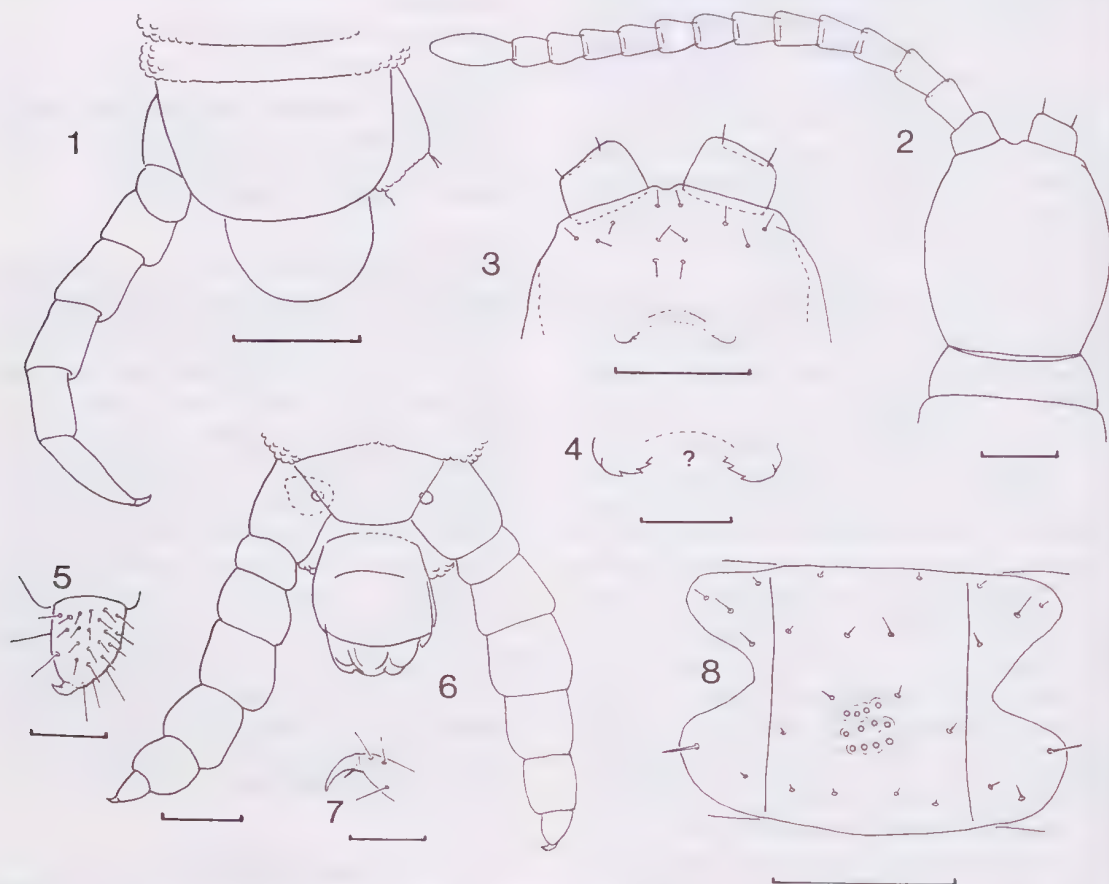
Diagnosis

With one coxal pore on each side, forcipules two thirds the length of the head capsule.

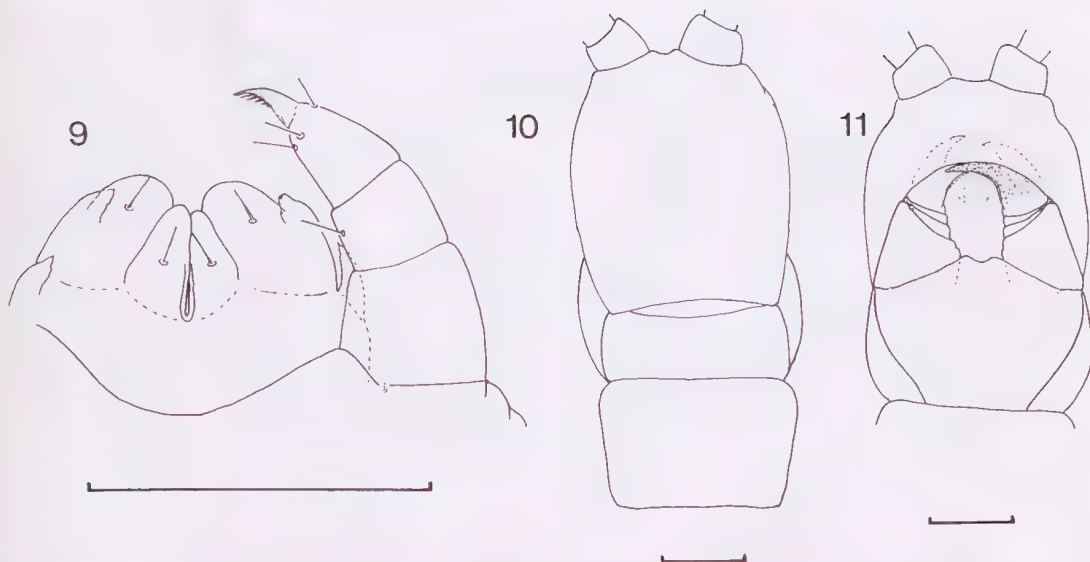
Description

Number of trunk segments: 41 and 43. Length: 13 mm.

Colour: colourless to yellowish white, head and forcipular segment slightly darker. Head capsule: slightly longer than wide, sides convex, a notch at the front between the antennae. Length about a third of that of the antennae (Figures 2, 10). Antennae: first segment very much wider than long; second to seventh, longer than wide; the rest wider than long or about equal except the last which is equal in length to the previous two (Figure 2). Forcipules: two-thirds the length of the head capsule. Seen from above the forcipules bulge outward at their base, beyond the margin of the head capsule (Figures 10, 11). Clypeus: with two post-antennary setae and a band of ten intermediate clypeal setae (Figure 3). Labrum: well marked sidepieces with at least three sharp teeth, is not well defined (Figure 4). Maxillae: first maxillae with two palpi per side; apical claw of the second maxillary telopodite with about seven spines on dorsomedial edge (Figure 9). Pore-groups: from first to 16th segment, gland openings



Figures 1–8 *Australoschendyla capensis* sp. nov., ♀ WAM 92/1318 (Figures 1–4, 7, 8); ♂ WAM 92/1322 (Figures 5, 6): 1, last trunk segment, from above; 2, head and antenna, from above; 3, clypeus; 4, labrum, central area obscured; 5, metatarsus of last ♂ leg; 6, last trunk segment, from below; 7, apical claw of eighth right leg; 8, fourth segment with pore-group. Scale lines equal 0.1 mm except for Figures 4, 5 and 7 where they equal 0.05 mm.



Figures 9–11 *Australoschendyla capensis* sp. nov.: 9, first and second maxilla from below, ♀ WAM 92/1318; 10, 11, ♂ WAM 92/1322: 10, head and forcipular segment from above; 11, head and forcipular segment from below. Scale lines equal 0.1 mm.

form a circular group in posterior half of sternite (Figure 8). Last trunk segment: presternite constricted medially. Metasternite trapeziform. One coxal pore present on each side, partly covered by metasternite. Last legs of female quite slender with few setae while those of male are greatly swollen and densely covered below with short setae. Metatergite D-shaped (Figures 1, 5, 6).

Australoschendyla albanensis sp. nov.

Figures 12–22

Material Examined

Holotype

♂, Bald Head, Albany, Western Australia, Australia, 10 May 1969, D.D. Giuliani (WAM 92/1623).

Paratype

Western Australia: Australia: 1 ♀, same data as holotype (WAM 92/1624).

Diagnosis

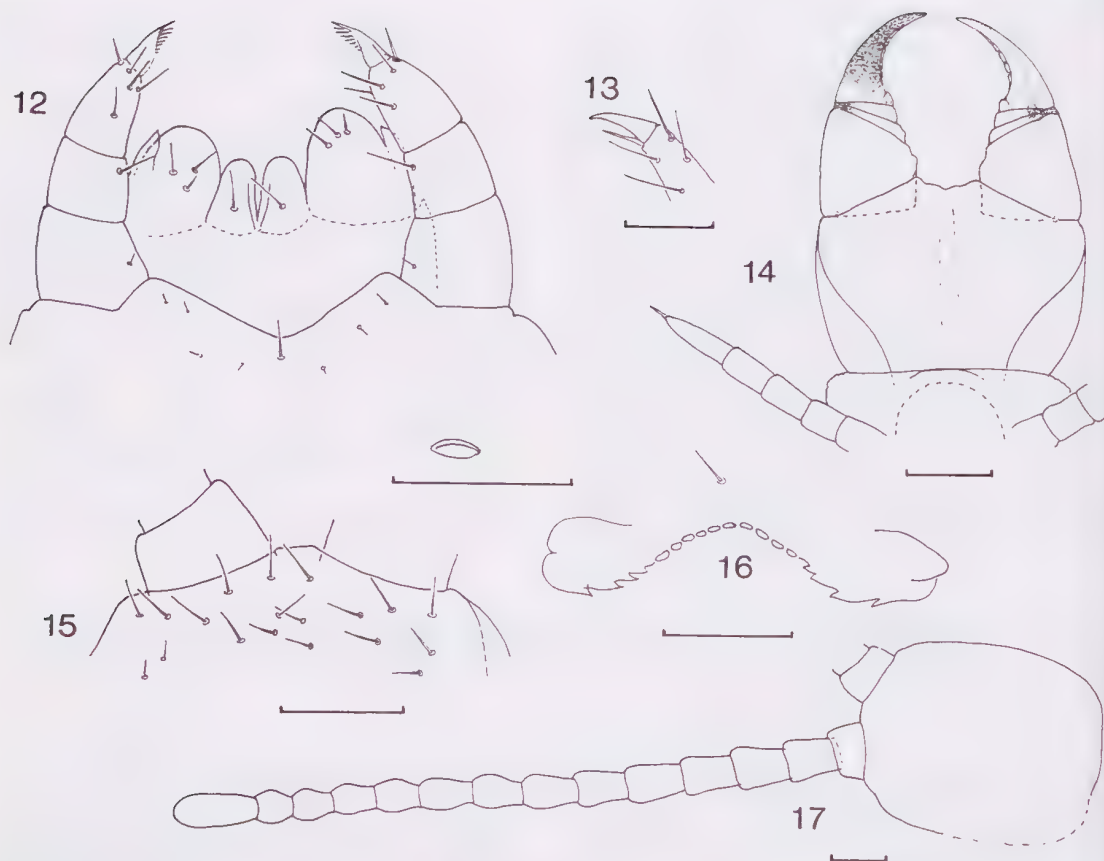
With two coxal pores on each side, forcipules equal in length to the head capsule.

Description

Number of trunk segments: 45 (♂), 47 (♀). Length: to ca. 15 mm.

Colour: colourless to yellowish white, head and

forcipular segment slightly darker. Head capsule: about equal in length and breadth, sides convex, length about a third of that of the antennae (Figure 17). Antennae: first segment very much wider than long, second to seventh longer than wide, the rest wider than long or about equal except the last which is equal in length to the previous two (Figure 17). Forcipules: equal in length to the head capsule. Seen from above the forcipules bulge outwards at the base but not as prominently as in *A. capensis* (Figure 14). Clypeus: with two post-antennary setae and a band of 16 or 17 intermediate clypeal setae. One, possibly two, prelabral setae (Figures 15, 16). Labrum: well marked sidepieces with four sharp teeth the midpiece bearing about 10 blunt teeth in an arch (Figure 16). Maxillae: first maxillae with two palpi on each side, apical claw of second maxillary telopodite with five or six spines on dorsomedial edge (Figure 12). Pore-groups: indistinct, but definitely present from second to 13th or 14th segment, gland openings forming a circular group in posterior half of segment (Figure 21). Last trunk segment: as in *A. capensis* the component sclerites are difficult to distinguish, but presternite appears to be split medially. Metasternite trapeziform and covering two coxal pores on each side. Female legs narrow with sparse setae, while male legs are fatter, though not as fat as in *A. capensis*, and covered ventrally with numerous short setae. Metatergite D-shaped (Figures 18, 19, 20, 22).



Figures 12–17 *Australoschendyla albanyensis* sp. nov., ♂ WAM 92/1623: 12, first and second maxilla, from below; 13, apical claw of sixth left leg; 14, forcipules, from below; 15, clypeus; 16, labrum; 17, head and antenna, from above. Scale lines equal 0.1 mm except for Figures 13 and 16 where they equal 0.05 mm.

DISCUSSION

Schendylids do not appear to be species diverse in the southwest Pacific area. A *Mesoschendyla* is known from Java (Attems 1914), an *Adenoschendyla* from Fiji (Chamberlin 1920), a *Plesioschendyla* from New Caledonia (Ribaut 1923) and a *Eucratonys* species from the Bismark Archipelago in New Guinea (Pocock 1898). These genera appear sufficiently distinct from each other and from *Australoschendyla* to justify their continuation as genera for the time being, but a revision of the Schendylidae and related families is much needed.

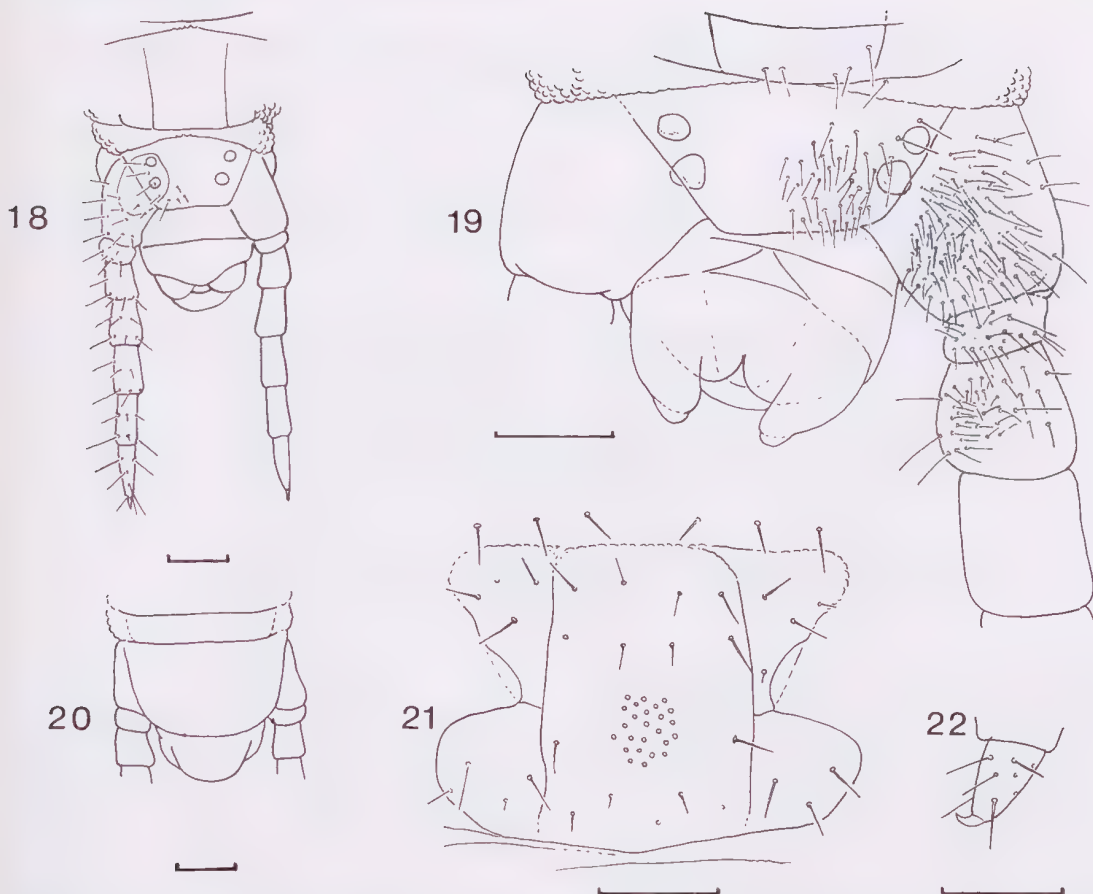
Both *A. capensis* and *A. albanyensis* are so far only known from their respective type localities. The two species can be distinguished by the length of the forcipules relative to the head capsule, by the number of coxal pores and the number of leg-pairs. These characters should be used with caution as there are likely to be more native schendylids found in Australia.

ACKNOWLEDGEMENTS

I wish to thank Mark Harvey of the Western Australian Museum who arranged for the loan of the specimens and the Norfolk Museum Service for providing research facilities. I would also like to thank Dr A.G. Irwin (Castle Museum, Norwich) for much help and discussion on taxonomic matters. Bob Mesibov gave helpful advice on an earlier draft of this paper.

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Figures 18–22 *Australoschendyla albanyensis* sp. nov., Figures 18, 20, ♀, WAM 92/1624; Figures 19, 21, 22, ♂, WAM 92/1623: 18, last trunk segment, from below; 19, part of last trunk segment, from below, showing details of setae; 20, last trunk segment, from above; 21, sixth segment with pore-group; 22, metatarsus of last a leg. Scale lines equal 0.1 mm.

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Biostratigraphy of Devonian microvertebrates from Broken River, North Queensland

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Abstract – Microvertebrate faunas from acid-leached residues from the Broken River region of north Queensland are dated by accompanying conodonts and span the interval *serotinus* (late Emsian) to *asymmetricus* (earliest Frasnian) zones.

Five major Devonian fish groups are represented: agnathan (thelodont), acanthodian (*Cheiracanthoides comptus*, *Nostolepis* cf. *costata*, *Nostolepis* spp., *Acanthoides* sp.), chondrichthyan (*Cladolepis* cf. *gunnelli*, *Ohiolepis* sp., phoeodont, indeterminate), placoderm (arthrodire, ptyctodontid), and osteichthyan (crossopterygian including *Onychodus* sp., palaeoniscoid, dipnoan).

Scales of *C. comptus* and *Cladolepis* cf. *gunnelli* both occur in horizons as young as *asymmetricus* Zone and are therefore longer ranging than previously reported. The stratigraphic range of the other Broken River forms falls within the range reported from elsewhere.

INTRODUCTION

The Broken River Group of North Queensland crops out as two shallow marine mixed carbonate platforms (northern Pandanus Platform and southern Dosey–Craigie Platform) covering approximately 320 square kilometres; it comprises five fossiliferous formations dated by conodonts as ranging from mid Emsian to earliest Frasnian (Mawson and Talent 1989). In the south (Figure 1), there are two limestone formations (Lomandra and Dosey limestones), and three mudstone/shale/siltstone units with nodular limestones (Bracteata Formation, Papilio Formation with associated Spanner Limestone Member, and Mytton Formation with associated Stanley Limestone Member); details of stratigraphy are given in the legend to Figure 1. Environments of deposition are interpreted as shallow marine (Lomandra Limestone, Mytton Formation), protected muddy shelf (Papilio Formation), deeper water muddy shelf (Bracteata Formation), shallow carbonate shelf (Dosey Limestone, Spanner Limestone), and carbonate shoal (Stanley Limestone) (Mawson and Talent 1989).

Previous work on the Broken River Group has resulted in reports of both microvertebrates and macrovertebrates. Reported from Early Devonian horizons are acanthodian scales and platelets, including *Nostolepis* sp., buchanosteid and radotinid tesserae, onychodontid teeth and an endemic turiniid from the Martins Well Limestone (Turner 1991, 1993), dated by conodonts as *pesavis-sulcatus* zones (Mawson *et al.* 1988; Withnall and Jell 1988). Middle Devonian forms reported are

more diverse: antiarchs *Wurungulepis denisoni*, represented by scales, fin bones, and articulated trunk armour, and skull and dermal bones of *Nawagiaspis wadeae* from Eifelian and Givetian horizons (Young 1990); *Cheiracanthoides comptus* scales, onychodontid teeth and palaeoniscoid remains from the Eifelian–Givetian Fish Hill, and a phoeodont tooth from the Papilio Formation (*varcus* Zone) (Turner 1993); acanthodians *Acanthodes* sp., and an indeterminate ischnacanthid, chondrichthyan *Ohiolepis* sp., thelodont *Turinia* sp., placoderms cf. *Pterichthyodes* sp. and indeterminate asterolepidoid, brachythoracid and rhenanid? remains, dipnoan cf. *Chirodipterus* sp., onychodontid *Onychodus* cf. *sigmoides*, and palaeoniscoid *Ligulalepis toombsi* (Long and Turner 1984); and acanthodian *Machaeracanthus* sp., placoderms *Atlantidosteus* sp. and a new brachythoracid, and an indeterminate dipterid (Young 1993). A 50mm-long crossopterygian lower dentary, as yet undescribed but probably *Onychodus* sp., was recovered in 1993 from near Fish Hill, from a horizon dated by associated conodonts as close to the *costatus/australis* boundary (De Pomeroy *et al.* 1994).

For details of geology, interpreted depositional environment and conodont biostratigraphy, see Mawson and Talent (1989).

RESULTS OF STUDY

Twenty sections (comprising 586 samples, each weighing approximately 1 kg) were measured from the Dosey–Craigie Platform and the southernmost

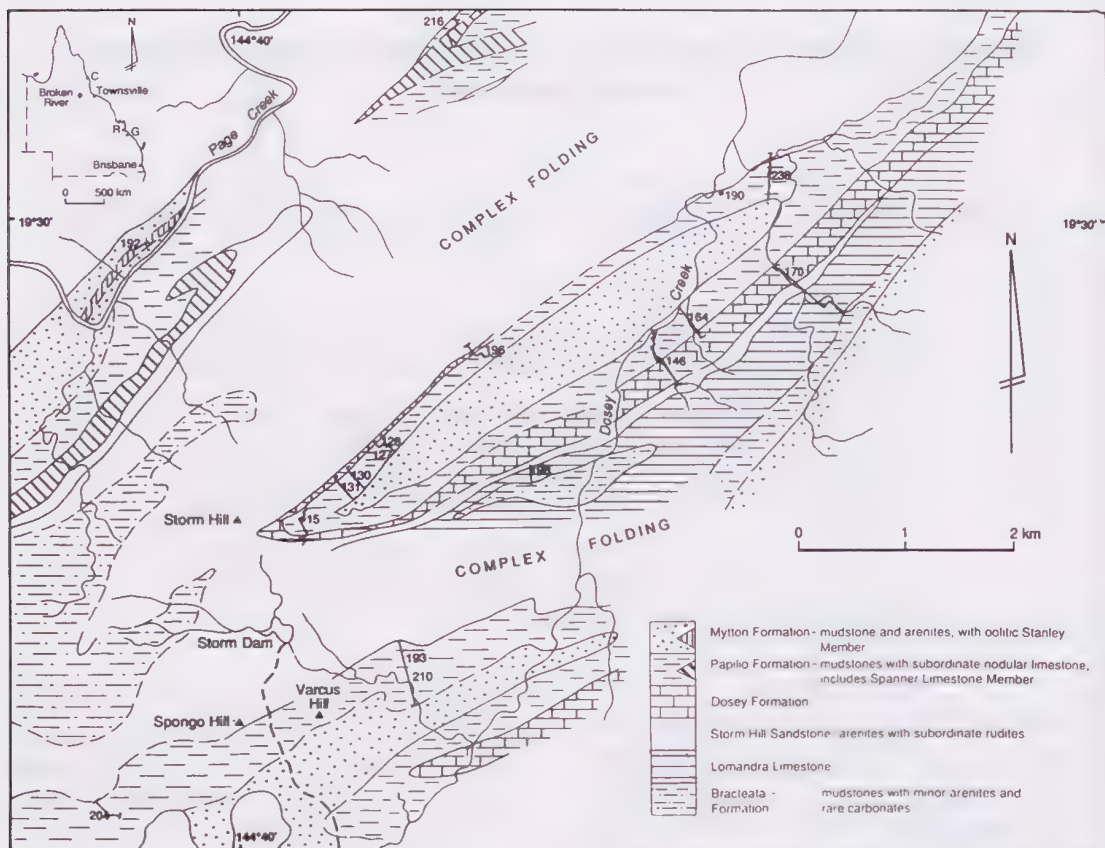


Figure 1 Broken River Group in the Dosey-Craigie Platform area showing location of stratigraphic sections. Sections bear prefix SD for Storm Dam (after Mawson and Talent 1989). Three sections are beyond the map boundaries: SD111 is approximately 3.6 km SW of Storm Dam; SAG is approximately 4.2 km east of Jessey Springs Hut; and SAGW is 94 m west of the original SAG section.

part of the Pandanus Platform. The microvertebrate faunas in the acid-leached residues from these samples have been precisely dated by the accompanying conodonts. Fish remains recovered include abundant acanthodian scales, chondrichthyan scales and teeth, onychodontid teeth; rare placoderm scales and bone fragments, onychodontid jaw fragments, and palaeoniscoid teeth; two onychodontid scale fragments, one palaeoniscoid scale, one thelodont scale, and one probable dipnoan toothplate.

The stratigraphic range of the forms reported here is compared with that from elsewhere. The presence of two forms in the Broken River Group extends the range later than that previously reported worldwide – the acanthodian *Cheiracanthoides comptus* and the chondrichthyan *Cladolepis* cf. *gunnelli*. Another acanthodian genus, *Nostolepis*, occurs later at Broken River than all other reported localities, with one exception. The ranges of the other forms recovered fall within the ranges reported from elsewhere (Figure 2).

SYSTEMATIC PALAEOONTOLOGY

Figured material is lodged in the palaeontological collections of the Queensland Museum (prefix QMF). Locality information is given by section number, followed by metres above base of section of lowest and highest productive sample. Figure 1 gives location of sections.

Superclass Agnatha

Subclass Thelodonti

Order Thelodontida

Thelodont indet.

Figures 6M, N

Material

One head scale (QMF 31856).

Locality

Section SAG/26.8m – Chinaman Creek Limestone; see Mawson *et al.* 1988, figure 13.

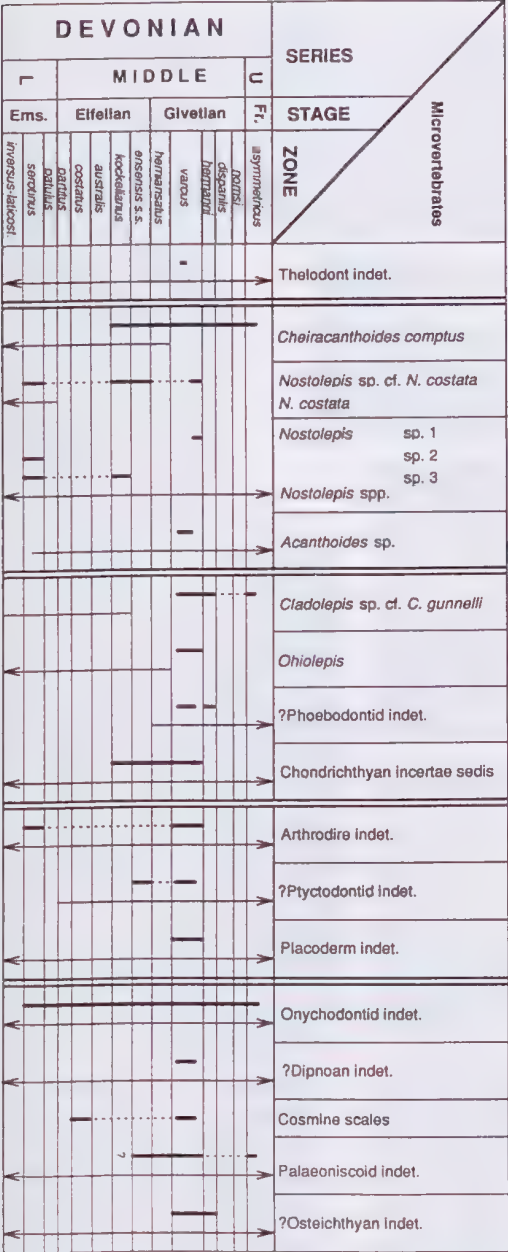


Figure 2 Stratigraphic ranges of microvertebrates discussed in text. Heavy line is range in Broken River Group; light line is range reported from other localities.

Stratigraphic level
Givetian (varcus Zone).

Remarks

All thelodonts have similar rounded head scales with undulating crown margins and radiating ribs, whereas trunk scales tend to be more distinctive

(Turner 1986). The Broken River scale resembles head scales of *Australolepis seddoni* Turner and Dring, 1981 described from the Frasnian Gneudna Formation in the Carnarvon Basin of WA, in its rounded shape, bifurcated ridges radiating from a central plateau on the crown, and size (0.5 mm), but lacks the deep furrows on the crown and the stepped ridges on the vertical crown surface typical of this genus. However, the specimen cannot be unequivocally assigned to *Australolepis*. It also resembles head scales of the turiniid genus *Turinia* (e.g. Turner *et al.* 1981, figure 7G). For the present the Broken River scale is assigned in open nomenclature to Order Thelodontida. Turner and Dring (1981) suggest that *Australolepis* and *Turinia* are related, the former possibly being derived from the Early Devonian *T. australiensis* Gross, 1971. Turner (pers. comm.) considers *Australolepis* may be a neotenous form of *T. australiensis*.

Description

The scale has a gently rounded central crown extending outwards in five low, broad ridges. One anterior and one lateral ridge bifurcate slightly at the distal end (Figure 6M). The neck is smooth and low. The elliptical base is larger than the crown, with a wide rounded rim surrounding the central shallow pulp cavity (Figure 6N).

Discussion

Thelodonts, most commonly turiniids, have been reported from Australian localities ranging in age from close to the Siluro-Devonian boundary to the early Frasnian; these are listed by Long and Turner (1984) and Young (1993, 1995), and figured by Pickett *et al.* (1985), Turner *et al.* (1981), Young and Gorter (1981), Turner (1986, 1991, 1993), Young *et al.* (1987), and Long *et al.* (1988). No thelodont scales from the Broken River region are described or figured in the literature, but Young (1995) reports an endemic turiniid from the *pesavis-sulcatus* Martins Well Limestone, and Turner (1993) mentions, from the Broken River Group, a Lochkovian *Turinia australiensis* morphotype, and turiniid and nikoliviid-like scales of no specified age.

Subclass Acanthodii Owen, 1846
Order Climatiida Berg, 1940
Family Climatiidae Berg, 1940
Cheiracanthoides Wells, 1944

Type species
C. comptus Wells, 1944.

Diagnosis
Scales with flat or slightly convex crown,

extending beyond base posteriorly, ornamented with parallel or slightly radiating rounded ribs, usually only on anterior part of crown. Neck low, clearly separated from both base and crown, with small canal openings on front and back. Base convex, usually extends anterior to crown, concentrically striated. Mesodentine crown, with Stranggewebe in posterior half, has concentric, radial and ascending vascular canals. Tubules on top of the crown grouped into tufts in the furrows, with side branches extending into the ridges. Base of cellular bone.

Cheiracanthoides comptus Wells, 1944

Figure 3A–D

Material

280 scales (QMF 31819, 20 + 278 others).

Localities

SD15/59.1–113m, SD128/54.3–201.5m, SD130/32.5–73.1m, SD131/92.1m, SD146/418m, SD164/117.7–124.1m, SD170/710m, SD192/0–50m, SD193 (spot sample), SD204/115.9–120m, SD210/69.7–132.3m, SD216/26.7–95.3m, and SAG/26.8–121.9m; Lomandra, Stanley, Spanner and Chinaman Creek limestones, and Papilio Formation.

Stratigraphic range

Eifelian (*kockelianus* Zone) to earliest Frasnian (*asymmetricus* Zone).

Remarks

The scales have the flat or slightly convex crown with posteriorly converging ridges, the low indented neck, and convex base, described by both Wells (1944) in the original diagnosis, and by Denison (1979) as being typical of this genus. The Broken River scales are a similar size to those of Wells (1944).

Description

The scales have four to eleven radiating or subparallel rounded ridges on the anterior part of the crown. The anterior edge of the crown has a distinct rim (Figures 3A, C) that separates the flat crown from the indented neck, and connects the front edge of the coronal ridges; this is particularly visible in side view (Figure 3B). All specimens have a diamond-shaped, convex base. The crown extends posteriorly beyond the base, in some specimens further (Figure 3D) than in others (Figure 3B). In most of the scales, the crown length and width is approximately equal, while the scale height is approximately one-third to one-half of the length/width measurement. The size range of the scales is 0.5–0.9 mm long, 0.4–1 mm wide, and 0.2–0.5 mm high. Thin sections reveal the typical

Nostolepis-type histology, with a pyramid-shaped base of cellular bone showing concentric growth zones, and a crown with ascending and concentric vascular canals (Denison 1979, figures 9A–C and 10B), however preservation is insufficient in the prepared thin sections to reveal whether tubules are grouped into tufts in the furrows, a feature distinguishing this genus from *Nostolepis* (Denison 1979).

Discussion

Wells (1944) separated scales of this morphological type into six species in two genera. These were subsequently amalgamated into the single species *C. comptus* by Gross (1973), who considered the morphological differences intra-specific.

The anterior coronal rim found on all Broken River specimens is not specified by Wells (1944) as a character of the genus, but his illustrations (figures 4a–k, 5a–e, and especially the side view in figure 4c) show a clear delineation between the flat crown and deeply indented neck. Some later illustrations of *C. comptus* also show the rim (e.g. Gross 1973, plate 26 figures 24–26; Vieth-Schreiner 1983, plate 4 figures 32–33; Valiukevicius 1985, plate 8 figures 4–5). In contrast, other specimens have the coronal ridges running down the anterior edge of the scale to where the neck area joins the base (e.g. Giffin 1980, figure 5; Gross 1973, plate 27 figure 2c; and *Cheiracanthoides* cf. *comptus* illustrated by Boucot *et al.* 1989, text-figure 19). In these latter two examples the crown, in side view, appears thicker than the crown of specimens with the anterior rim. It is possible that this type of scale, without the anterior coronal rim, belongs to a different taxon, or at least occurs on a different region of the body.

An acanthodian scale with some morphological similarity to the Broken River specimens, including the anterior rim on the crown, has been figured and described as *?Gomphonchus* sp. by Long *et al.* (1988, figure 2F, G). Those authors discuss the differences between *Gomphonchus* and *Cheiracanthoides*, and these differences are sufficient to separate *Gomphonchus* and the Broken River material.

Scales assigned here to *C. comptus* Wells, 1944 are the most common acanthodian microvertebrates in the Broken River material occurring in horizons from Eifelian (*kockelianus* Zone) to earliest Frasnian (*asymmetricus* Zone). Specimens from Australian localities are figured by Giffin (1980 figure 5) and Turner (1991, plate 2A, F, plate 5C). The cosmopolitan genus has been reported elsewhere from the Early and Middle Devonian, particularly the Emsian and Eifelian (e.g. Wells 1944; Vieth 1980; Valiukevicius 1979, 1985), and also from the lowermost Givetian (*hemiansatus* Zone – Vieth-

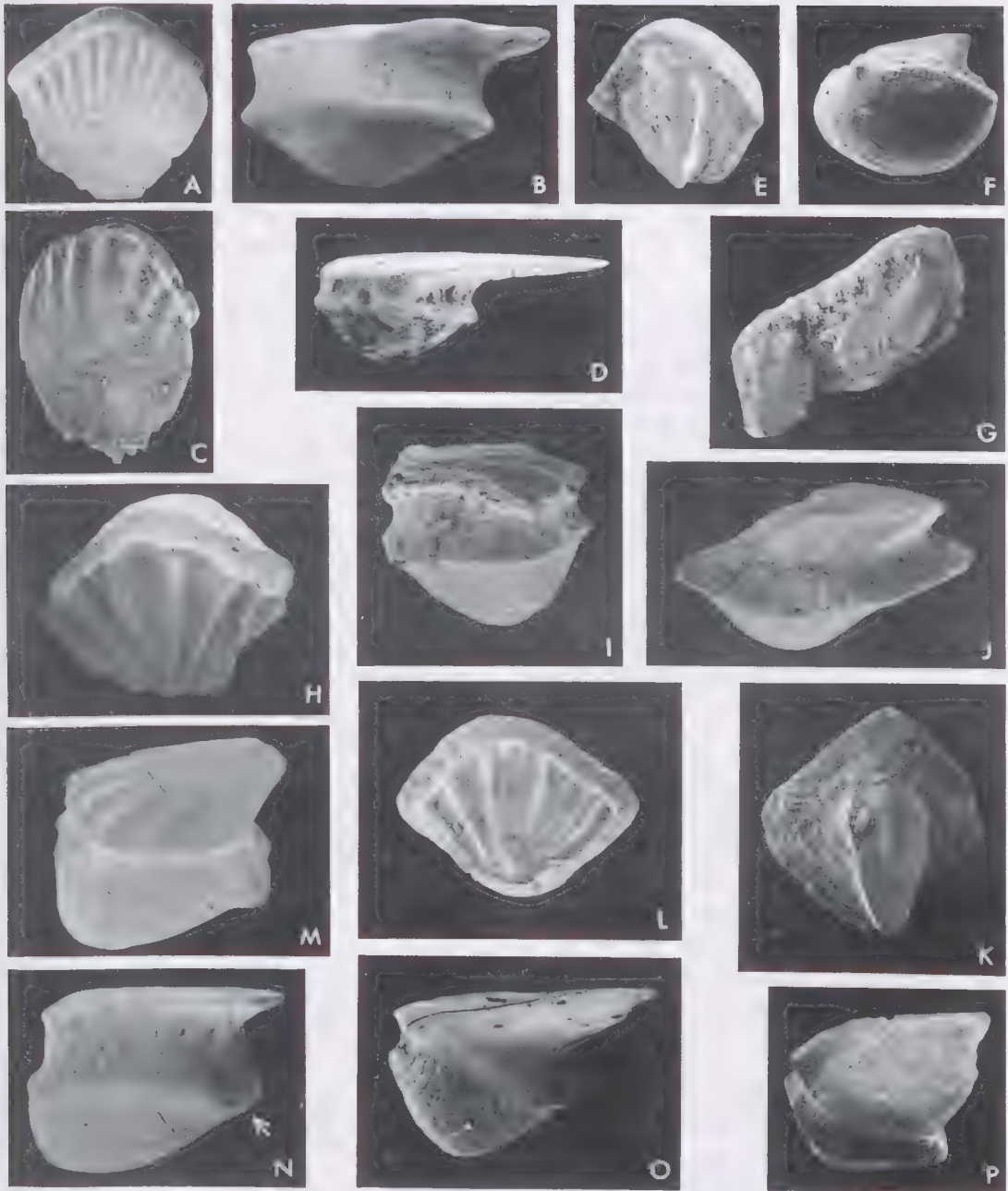


Figure 3 A–D, *Cheiracanthoides comptus* Wells, 1944. A,B, crown (x50) and lateral (x75) views of scale QMF 31819, SD204/120 m. C,D, crown (x50) and lateral (x75) views of scale QMF 31820, SD210/104 m.
E–G, *Nostolepis* sp. 2. E, crown view x90, F, latero–basal view x100 of scale QMF 31821, SD170/182–188.5 m. G, crown view of double scale QMF 31822, x75, SD170/182–188.5 m.
H,I,L, *Nostolepis* cf. *costata* Goujet, 1976. H,I, crown and lateral views of scale QMF 31823, x60, SD170/200 m. L, crown view of scale QMF 31824, x90, SD204/120 m.
J,K, *Nostolepis* sp. 1. J, lateral view x90, K, crown view x75, of scale QMF 31825, SD210/195.7 m.
M,N, *Nostolepis* sp. 3. Crown and latero–posterior views of scale QMF 31826, x60, SD170/700 m (appr).
O,P, *Acanthoides* sp. O, anterior view x100, P, crown view x90 of scale QMF 31827, SD204/120 m.

Schreiner 1983). There are no reports of these scales occurring elsewhere in horizons of *varcus* Zone or younger age. Correlation with associated conodonts at Broken River gives a definite age range for the species in eastern Australia, possibly the youngest occurrence globally.

Nostolepis Pander, 1856

Type species

N. striata Pander, 1856.

Remarks

In the almost 150 years since Pander erected the genus, scales and platelets with widely varying morphology have been ascribed to *Nostolepis*. Denison (1979) describes *Nostolepis* scales as being 'variously ornamented with converging or parallel ridges, or with strong ribs', and, along with more recent workers, emphasises the importance of histological examination to reveal the distinctive *Nostolepis*-type structure. Histological features typical of the genus include wide vascular canals, mesodontine in the crown, and Stranggewebe (C. Burrow, pers. comm.). It is likely that some specimens described as *Nostolepis* are a different taxon, and indeed, the whole concept of the genus is in need of review and clarification. However, the specimens from Broken River are ascribed to this genus for the present because of similarities with published forms (see below).

The genus is commonly found worldwide in Late Silurian and Early Devonian horizons (Obruchev and Karatajute-Talimaa 1967; Gross 1971; Goujet 1976; Denison 1979; Vieth 1980; Blicek *et al.* 1984; Wang 1984; Macadie 1985; Valiukevicius 1985, 1988; Mader 1986; Pan Jiang and Dineley 1988; Turner and Murphy 1988; Boucot *et al.* 1989; Forey *et al.* 1992; Lelievre *et al.* 1993). *Nostolepis* has been reported from later than Early Devonian at only two other localities (Valiukevicius 1985, 1988) – *N. kernavensis* Valiukevicius, 1985 from the Upper Narva Regional Substage (Narov "Gorizont") of Lithuania, broadly equivalent to *costatus* Zone (Reshenie 1990), and *Nostolepis* sp. no. 11 from the Frasnian Gauja Regional Stage of the Baltic Region of the former USSR. Scales assigned to *Nostolepis* have been reported from several Australian Early Devonian localities – Cravens Peak Beds of Queensland, Tumblong, Trundle Beds, Condobolin Formation and Yarra Yarra Creek Group of NSW, Silverband Formation, Coopers Creek Limestone, Tyers and Buchan in Victoria (Long and Turner 1984; Pickett *et al.* 1985; Turner 1991). No *Nostolepis* scales have been figured or described from the Broken River region, but *N. striata* is recorded as occurring in the Late Silurian Martins Well Limestone, and at Broken River Gorge, in strata of no given age (Long and Turner 1984). Two

nostolepid scales in *varcus* Zone at Broken River (*Nostolepis* cf. *costata* and *Nostolepis* sp. 1 – see below) are thus, with the exception of the Frasnian species from the Baltic, the youngest recorded occurrence of the genus.

Nostolepis cf. *costata* Goujet, 1976

Figures 3H, I, L

Material

Nine scales (QMF 31823, 4 + seven others).

Localities

SD128/78m, SD170/200–710 m, SD204/120 m and SAGW/20 m; Lomandra and Chinaman Creek limestones, Papilio Formation.

Stratigraphic range

Emsian to Givetian (specimens occur in *serotinus*, *kockelianus*, *ensensis* and *varcus* zones).

Remarks

These scales are similar to those of *N. costata* Goujet, 1976, described from the Early Devonian of Saint-Céneré, France. However, the crown of the Broken River scales lacks lateral blades with a denticulate margin as in *N. costata*. This may simply be the result of abrasion, as all specimens show some signs of wear. Also, the Broken River scales are smaller than those from France; the latter reach up to about 2 mm in length and width (Goujet 1976).

These scales differ from those assigned to *C. comptus* (above) in the extension of the coronal ribs to the posterior point, the presence of bifurcations or short secondary ribs anteriorly, and the extension of the base beyond the crown on all sides.

Description

The flat crown, rounded anteriorly and tapering to a point posteriorly, has four or five strong, radiating ribs extending to the posterior point. These ribs may bifurcate at the anterior margin (Figure 3H), and there may be smaller, short secondary ribs between the main ones (Figure 3L). The shallow neck is indented and is deeper at the back (Figure 3I). The diamond-shaped base is strongly convex and extends beyond the crown on all sides (Figure 3L). Size of unbroken specimens is in the range 0.5–0.7 mm in length and width, with depth about 0.4–0.5 mm. Histological sections were not attempted because of the small number of specimens and the generally poor state of preservation.

Discussion

Forms assigned to *N. costata* are said to be

common in Lochkovian to Emsian limestones of NSW (Turner 1991); no examples are illustrated. The Broken River scales occur in horizons as young as Givetian; one specimen is from SD204/120m, in upper *varcus* Zone, dated by presence of conodonts *Polygnathus varcus*, *P. latifossatus* and *P. timorensis*.

Nostolepis sp. 1

Figures 3J, K

Material

1 scale (QMF 31825); other scales possibly belong to this taxon but are too abraded to assign with certainty.

Locality

SD210/196.4 m; Papilio Formation.

Stratigraphic level

Givetian (Upper *varcus* Zone).

Remarks

This scale differs from those assigned above to *Nostolepis* cf. *costata* in crown ornament: a central raised section, tapering posteriorly and with oblique ridges on the lateral edges, and with a flat, broad rim.

Description

The diamond-shaped scale is 0.5 mm long and wide, and 0.3 mm high. The central part of the crown is raised and smooth except for a median ridge (Figure 3K); the sloping lateral edges of this raised section have several oblique ridges (Figure 3J). The base is strongly convex. A distinct projecting rim encircles the scale at the crown/base junction.

Discussion

A similar nostolepid scale from the Pragian-early Emsian Jauf Formation of Saudi Arabia is figured by Boucot *et al.* (1989, figure 20a,b). Turner and Murphy (1988, figure 2.2) illustrate the crown view of a *Nostolepis*-type scale, which they consider resembles scales of *N. striata*, from the Windmill Limestone of the Simpson Park Range, Eureka County, Nevada; this scale is similar to the Broken River specimen. It is noted, however, that these figured scales are from the Early Devonian, whereas the Broken River specimen is dated Middle Devonian.

Nostolepis sp. 2

Figures 3E–G

Material

51 scales (QMF 31821,2 + 49 others).

Localities

SD170/185–200 m; Bracteata Formation.

Stratigraphic level

Emsian (*serotinus* Zone).

Description

These scales have the same diamond shape in crown view and deeply convex base as *Nostolepis* sp. 1, and a similar central, raised sloping section on the crown. They differ in having the raised crown section more triangular with the central ridge more pronounced and extending further anteriorly (Figure 3E), in the sloping lateral edges of the raised section being unornamented, and in lacking the protruding rim where the crown joins the base. The lateral and posterior corners of the crown are slightly extended into points (Figure 3E), while the anterior corner is rounded. Scales of this type are slightly smaller than *Nostolepis* sp. 1 – length and width are approximately 0.3 mm, and height about 0.2 mm. Fifty of the scales were recovered from the same sample (185m above base of section SD170). It is possible, therefore, that they are from a single fish, but preservation is not adequate to detect a noticeable variation among them, with the exception of the double scale illustrated in Figure 3G.

Discussion

The *Nostolepis*-type scale from the Lochkovian of Nevada figured by Turner and Murphy (1988, figure 2.3) bears a slight resemblance in crown view to the Broken River specimens, in the tripartite central raised section on the crown and in the overall diamond-shaped outline.

Nostolepis sp. 3

Figures 3M, N

Material

Three scales (QMF 31826 + two others).

Locality

SD170/185,710 m; Bracteata Formation, Dosey Limestone.

Stratigraphic range

Emsian (*serotinus* Zone) and Eifelian (*kockelianus* Zone).

Remarks

These scales differ from those of *Nostolepis* cf. *costata* discussed above by having a flat crown with low subparallel ridges only in the anterior half, in contrast to the strong, radiating ridges extending to the posterior of the crown in *Nostolepis* cf. *costata*, and in the lateral rounded projection. They

differ from *Nostolepis* sp. 1 and sp. 2 in the crown ornamentation.

Description

The crown is flat, rounded anteriorly and tapering posteriorly, with six subparallel ridges, the central two of which bifurcate at the anterior margin (Figure 3M). The neck is indented at anterior and posterior, with about six small holes at the posterior. The neck area is thickened laterally, extending into a rounded projection at each side of the scale where the neck joins the base. At the posterior corner, the lower edge of the neck dips to form a downward-curving arc (arrow in Figure 3N). The base is deeply convex, with the greatest depth towards the anterior end of the scale. Both length and width are approximately 0.6 mm, and depth of the scale is approximately 0.4 mm. Recovery of only three specimens precludes histological examination.

Order Acanthodida Berg, 1940

Family Acanthodidae Huxley, 1861

Acanthoides Brotzen, 1934

Diagnosis

Acanthodian scales with smooth, glistening, usually more or less convex crown, translucent on edges, quadrangular to rhomboidal in outline, with short neck and thick, rounded inverted pyramidal base (Wells 1944:28).

Acanthoides sp.

Figures 3O, P

Material

Eleven scales (QMF 31827 + ten others).

Locality

SD204/120 m; Papilio Formation.

Stratigraphic level

Givetian (Middle *varcus* Zone).

Description

The crown of the scales is flat and unornamented (Figure 3P), the pointed posterior edge extends beyond the base, and the anterior and lateral edges incline slightly ventrally. The neck is deep and indented, and the highly convex base is deepest towards the anterior of the scale (Figure 3O). These scales, together with *Nostolepis* sp. 2 described above, are the smallest of the acanthodian scales recovered, with length and width 0.3–0.4 mm, and height about 0.2 mm. The better-preserved scales have a transparent honey-coloured crown and an opaque black base; other scales are totally black.

Discussion

Confusion has arisen in the literature between scales assigned to the genera *Acanthodes* Agassiz, 1833 and *Acanthoides* Brotzen, 1934. Wells (1944) recognises *Acanthoides* as a form genus, distinct from the Carboniferous *Acanthodes*, whereas Denison (1979) acknowledges *Acanthodes* from the Carboniferous and Permian, but suggests that forms assigned to various species of *Acanthoides* are in fact synonymous with *Gomphonchus* Gross, 1971 and possibly *Nostolepis* Pander, 1856. Storrs (1987: 365) and Turner (Boucot *et al.* 1989:572) discuss this problem, Turner suggesting that the whole classification of smooth-crowned acanthodian scales from the Middle Devonian needs revision. The scales described here are assigned to *Acanthoides*, using Wells's concept of a form genus for smooth-crowned scales considered too old to belong to the Carboniferous and Permian genus *Acanthodes*.

The Broken River scales strongly resemble specimens named *Acanthodes? dublinensis* figured by Gross from the early Middle and late Late Devonian (1973, plate 27, figures 8–11 and 16–17), by Vieth from the Emsian and Eifelian (1980, plate 8, figures 21–22), and by Storrs from the Givetian and Frasnian (1987, figures 5–6), although these illustrations more closely fit the description given by Wells (1944:29) for *Acanthoides dublinensis* than that by Stauffer (1938:442) for *Acanthodes? dublinensis*. In Australia, the genus *Acanthodes* has been reported, but not described or figured, from the Middle Devonian of Broken River, and Early Carboniferous of Victoria and Queensland (Long and Turner 1984). Also from Australia are scales of *Howittacanthus kentoni* from the Frasnian Mt Howitt locality in eastern Victoria (Long 1986). These small scales have a flat unornamented crown and are morphologically indistinguishable from those of *Acanthodes* (Long 1986).

Class Chondrichthyes Huxley, 1880

Infraclass Elasmobranchii Bonaparte, 1838

Order Cladoselachida Dean, 1894

Family Cladoselachidae Dean, 1909

Cladolepis Wells, 1944

Cladolepis cf. *gunnelli* Wells, 1944

Figures 4A–C

These specimens have been described and discussed elsewhere (De Pomeroy 1994). They are included here because the range of this form at Broken River is longer than previously reported.

Scales of *Cladolepis* cf. *gunnelli* Wells, 1944 (Figures 4A–C) occur in Givetian to earliest Frasnian (Middle and Upper *varcus*, *hermanni*–

cristatus and *asymmetricus* zones) horizons at Broken River. *Cladolepis* sp. scales have been reported from the early Eifelian Lauch Formation of Germany (Vieth-Schreiner 1983) in horizons of *patus* Zone age (Weddige 1977); the late Emsian Santa Lucia Formation of Spain (Mader 1986); and the Middle Devonian of North America (Wells 1944; Gross 1973) in horizons dated *kockelianus* Zone or earlier (Klapper and Johnson 1980). None of these occurrences is as young as the Broken River specimens. Scales possibly belonging to the genus are reported from the middle Givetian-early Frasnian Holy Cross Mountains of Poland (Liszkowski and Racki 1992), and the *gigas* Zone (early Frasnian) Mostyn Vale Formation of NSW (Turner 1993).

Ohiolepis Wells, 1944

Ohiolepis sp. Wells, 1944

Figures 4D–G

These specimens have previously been described and discussed (De Pomeroy 1994). They are included here simply as part of the comparison of ranges of the Broken River fauna with occurrences reported elsewhere. Scales assigned to the genus are present in horizons of Middle and Upper *varcus* zones at Broken River (Figure 2), which is later than other reports. However, the concept of the genus appears to have become confused over the years (see De Pomeroy 1994) and is in need of revision, so the apparent late appearance of these scales at Broken River is at present considered of little significance.

Order Euselachii Hay, 1902

Superfamily Ctenacanthoidea Zangerl, 1981

Family Phoeodontidae Williams, 1985

?Phoeodontid indet.

Figures 4H, I

Material

Two broken cusps (QMF 31831 and one other).

Localities

SD128/134.1 m and SD164/124.1 m; Papilio Formation.

Stratigraphic range

Givetian (Middle *varcus* and *hermanni-cristatus* zones).

Remarks

The Broken River fragments are similar to cusps of *Phoeodus australiensis* and *P. politus* from the

late Famennian of Thailand discussed and figured by Long (1990 figures 2–4). These two species have three- and four-cusped teeth with, respectively, three to four and seven to ten coarse vertical striae on the lingual surface (Long 1990), compared with six striae on the Broken River specimens. The Broken River specimens also resemble cusps of *P. bifurcatus*, where the labial face of some cusps bears strong, subparallel ridges, as found at late Frasnian localities in the South Urals (Ginter and Ivanov 1992: figures 4A–F, 5D–H). Turner (1982, figure 6A) illustrates a 3-cusped tooth assigned to *Phoeodus* cf. *politus*, from the Famennian Burdekin Star Shelf in Queensland. These cusps have longitudinal, raised striae, similar to the ornament on the Broken River specimens.

Description

The conical fragments are less than 1 mm long, with a small central pulp cavity, six straight longitudinal ridges on one side, and a circular cross-section. Under high magnification (Figure 4I), finer oblique striations are visible between the ridges; the other side of the cusp is smooth. Both fragments are apical ends of cusps, and are not curved.

Discussion

Phoeodont teeth are known from the Middle Devonian to Late Carboniferous (Zangerl 1981). Other reported Middle Devonian phoeodont teeth include the two species of *Phoeodus* erected by Wells (1944) from North American material, *P. floweri* with three to five slightly spiralling striations on one side of the cusp, and *P. ? bryanti* with smooth cusps and ovoid cross-section, figured by Gross (1973: plate 34, figure 23, plate 35, figures 7–8); those of the middle and late Givetian of the Holy Cross Mountains in Poland (Liszkowski and Racki 1992, figures 3, 4L–N); and a Givetian tooth from section SD146 at Broken River, reported by Turner (1993).

Chondrichthyan incertae sedis

Figures 4J–L

Material

Sixty-one teeth (QMF 31832, 3 and 59 others).

Localities

SD15/115.6 m, SD127/43 m, SD128/68.6–132 m, SD130/25.5–109.3 m, SD164/40.2–80.8 m, SD210/75–104 m, SD216/25–106 m, and SAGW/20 m; Papilio Formation, Spanner and Chinaman Creek limestones.

Stratigraphic range

Givetian (*kockelianus* to *varcus* zones).

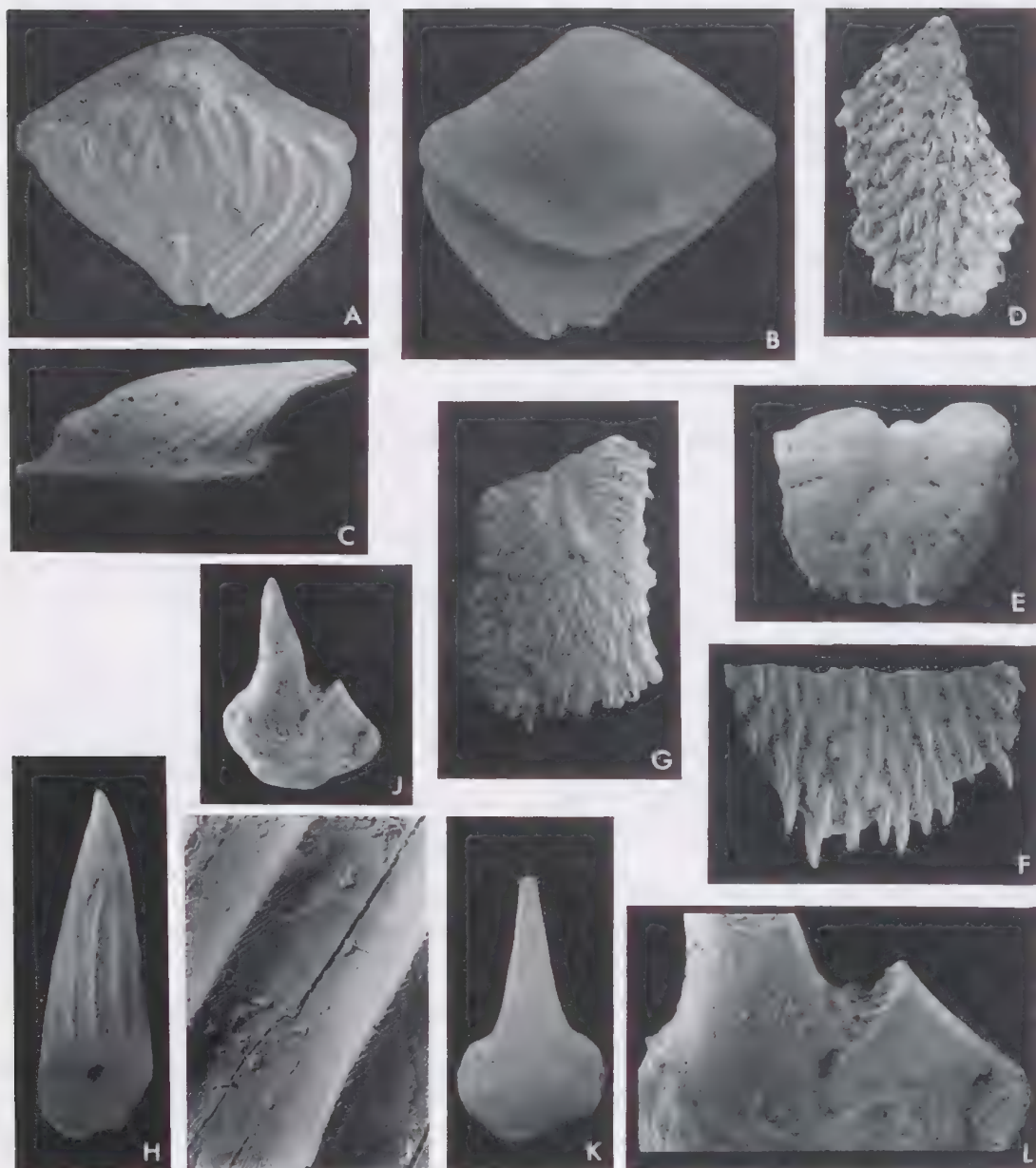


Figure 4 A–C, *Cladolepis* cf. *gunnelli* Wells, 1944. A,B, crown and base views x30, C, lateral view x40 of scale QMF26100, SD190/60.

D–G, *Ohiolepis* sp. Wells, 1944. D, crown view of scale QMF26103, x45, SD130/265.9 m. E, base view of scale QMF 31828, x45, SD204/120 m. F, crown view of broken scale QMF 31829, x60, SD204/120 m. G, crown view of scale QMF 31830, x45, SD204/120 m.

H,I, ?phoebodontid indet. H, x100, I, surface detail x220 of cusp QMF 31831, SD164/124.1 m.

J–L, chondrichthyan incertae sedis. K, lateral view of tooth QMF 31832, x55, SD15/187.6 m. J, lateral view x45, L, detail x110 of tooth QMF 31833, SD210/104 m.

Remarks

Few Palaeozoic chondrichthyan teeth figured in the literature are single-cusped, a condition considered by Zangerl (1981) to be the least specialised morphological type. One monocuspid form, however, is *Cobelodus aculeatus* (Cope) described by Zangerl and Case (1976) from the Late Carboniferous of North America; teeth from the upper dentition (Zangerl and Case 1976, figure 16; Zangerl 1981, figure 8E) are similar to the Broken River specimens in the single conical cusp being attached to a bulbous base, but differ in the cusp being longer and finely striated.

Figured teeth of *Antarctilamna prisca* and "*Xenacanthus*" sp. (the latter recently referred to a new genus *Portalodus* – Long and Young 1995) from the late Givetian or early Frasnian Aztec Siltstone in Antarctica (Young 1982, text-figure 3, plate 89, figures 1–4) bear a slight resemblance to the Broken River specimens. Histologically, the Broken River specimens have a similar structure to that described by Young (1982) for *Antarctilamna* teeth. However, the Antarctic teeth differ in being diplodont, in having the cusps curved, partly striated, perhaps with an accentuated striation or flattened side close to the base to form a cutting edge, and in the root being concave with a torus on the lingual side (Young 1982).

Description

The conical teeth are set centrally or towards one edge of a bulbous, subspherical base. One specimen (Figure 4J) from SD210/104 m in middle *varcus* Zone has a small second cusp; both cusps are broken distally. All other specimens are single-cusped. The cusps are about 0.4–0.5 mm long, smooth and uncurved, with a circular cross-section and blunt tip. Apart from the two-cusped specimen, the teeth are similar in size and shape; this lack of variation is common in Devonian elasmobranchs (Young 1982). The base has a ring of small holes close to the base of the tooth (Figure 4K). In some specimens, the central part of the base contains a spherical pulp cavity that extends a short distance into the cusp in a broad conical shape; in others, the base has no foramina or cavities.

Discussion

The samples containing these chondrichthyan teeth have also yielded numerous disarticulated scales, assigned to three new chondrichthyan form genera: *Gondwanalepis*, *Notiolepis* and *Aussilepis*, with respective ranges of *kockelianus* to younger than *varcus*, *mid-ensensis* to younger than *varcus*, and *ensensis* to younger than *varcus* (De Pomeroy 1994). As the stratigraphic ranges of these scales and that of the 61 teeth are similar, it is possible the teeth are from one of these genera.

Class Elasmobranchiomorpha

Subclass Placodermi

Order Arthrodira Gross, 1932

Arthrodire indet.

Figures 6G, H, J

Material

One possible arthrodire infragnathal (lower dermal jaw bone) (QMF 31852) and one scale (QMF 31853).

Localities

QMF 31852: SD198/67.6 m; Lomandra Limestone.

QMF 31853: SD170/200 m; Bracteata Formation.

Stratigraphic levels

QMF 31852: Givetian (*varcus* Zone).

QMF 31853: Emsian (*serotinus* Zone).

Remarks

This scale (QMF 31853) is dissimilar to the asterolepidoid antiarch *Wurungulepis* (see Young 1990, figure 13), the only other placoderm scale type described from this area. The ornament resembles that on scales of a buchanosteid arthrodire from Taemas (specimen CPC 16965, held at AGSO, Canberra). In the Broken River specimen the radiating ridges extend to the top of the tubercles, in contrast to the tubercles of CPC 16965, which are smooth in the centre and ridged only around the edges, but this scale type also occurs at Taemas (e.g. '*Ohioaspis tumulosa*' Giffin 1980, figure 3). Similar "buchanosteid"-type body scales are illustrated from the Lochkovian (*delta* Zone) of Nevada (Turner and Murphy 1988:962, figures 2.8–2.12).

Description

Fragment QMF 31852 (Figures 6G, H) measures almost 2mm long and just over 1mm high. Four spatulate denticles are ankylosed to the upper (dorsal) surface, with no obvious delineation between the material of the denticles and that of the bone. Two small foramina, probably for the passage of nerves or vessels (arrows in Figure 6H), are situated near the anterior margin of the bone. The ventral surface has a deep longitudinal groove, which would contain the meckelian cartilage if interpretation as an arthrodire infragnathal is correct. This groove starts a short way back from the blunt anterior tip of the bone, immediately posterior to a foramen (lower arrow in Figure 6H). The sides of this deep groove are composed of thin bone, in contrast to the more robust structure of the dorsal denticulate region and the solid anterior tip. One side extends further ventrally than the other (Figure 6G). Along one lateral surface a

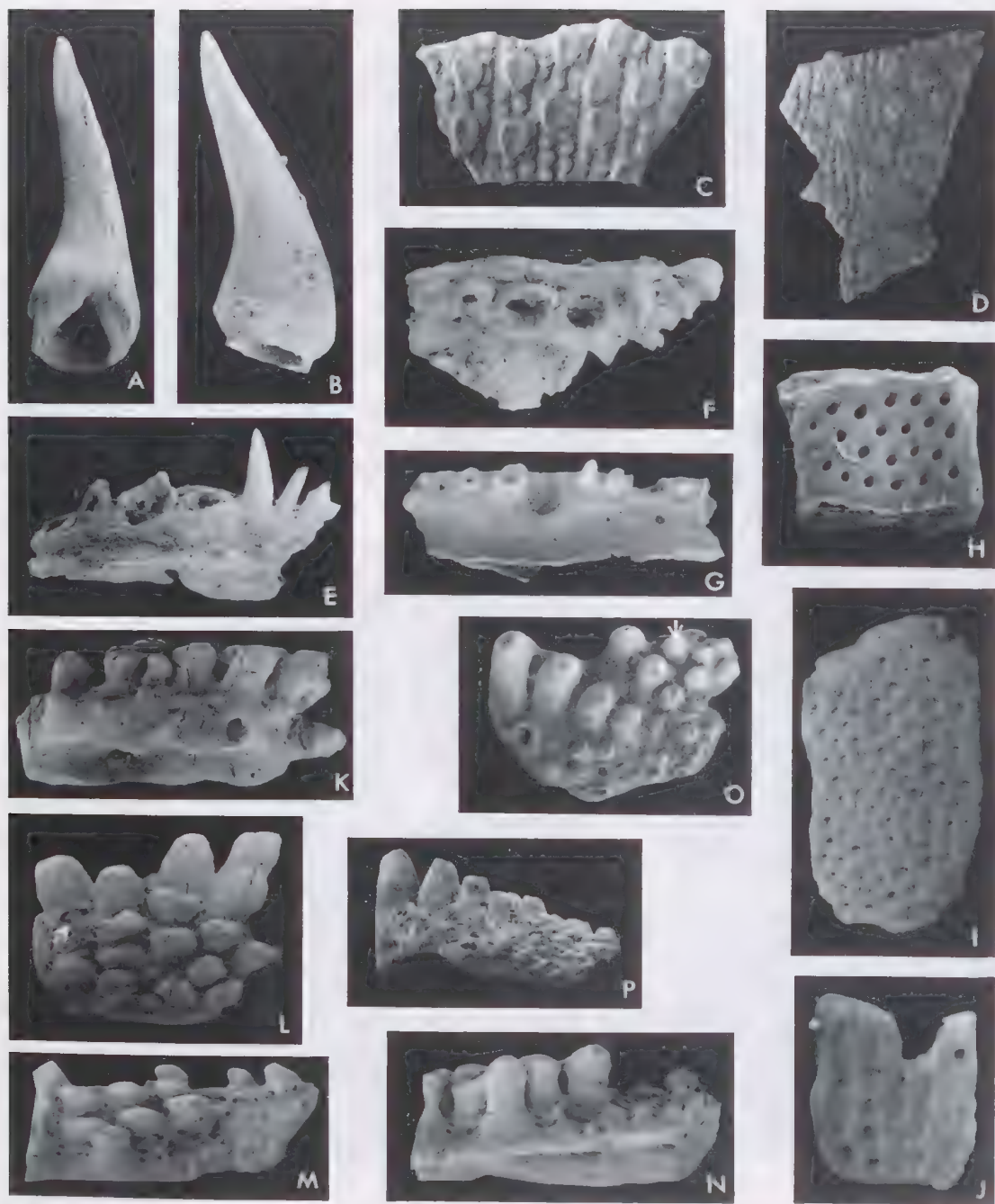


Figure 5 A–G, onychodontid indet. A, lateral view of tooth QMF 31834, x12, SD111/245 m. B, lateral view of tooth QMF 31835, x30, SD128/190 m. C,D, crown view of scale fragments. C, QMF 31836, x60, SD164/24.7 m. D, QMF 31837, x40, SD164/24.7 m. E, lateral and F, dorsal views of tooth-bearing bone fragment QMF 31839, x35, SD216/35 m. G, latero-dorsal view of tooth-bearing bone fragment QMF 31838, x30, SD210/87.7 m. H–J, cosmine scales, all crown view. H, QMF 31840, x30, SD15/148.5 m. I, QMF 31841, x30, SD204/120 m. J, QMF 31842, x60, SD210/87.7 m. K–N, ?osteichthyan indet. K, lateral view x50, L, dorsal view x45 of toothplate fragment QMF 31843, SD204/120 m. M, dorsal and N, lateral views of toothplate fragment QMF 31844, x45, SD204/115.9 m. O,P, ?dipnoan indet. probable toothplate. Crown and lateral views of QMF 31845, x30, SD131/117.7 m.

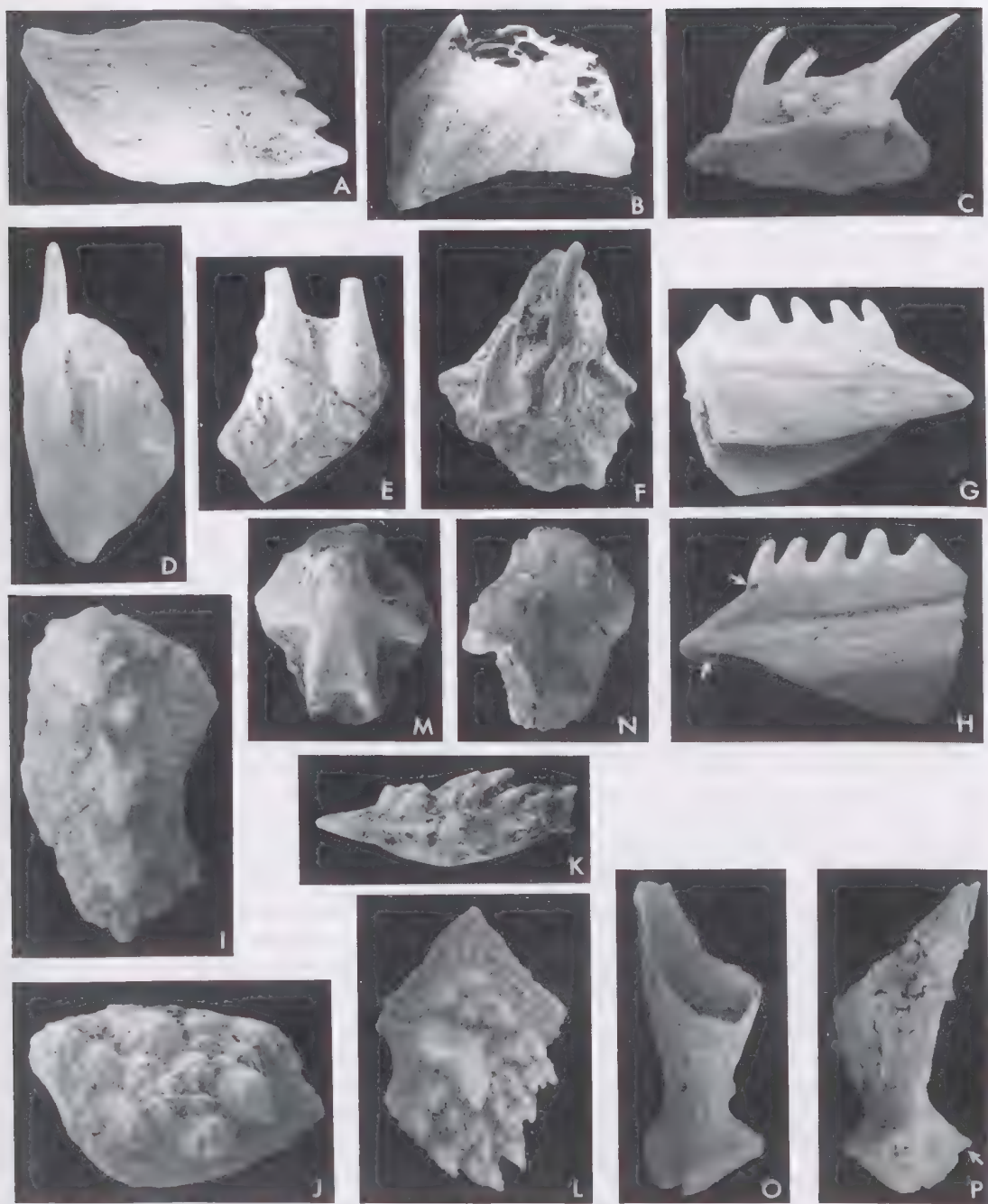


Figure 6 A, palaeoniscoid indet., crown view of scale QMF 31846, x30, SD192/60 m.
B, ?ptyctodontid indet., lateral view of probable supragnathal QMF 31847, x20, SD111/29 m.
C–F, palaeoniscoid indet. tooth-bearing plates. C, latero-basal view of QMF 31848, x75, SD204/95 m. D, top view of QMF 31849, x35, SD204/120 m. E, top view of QMF 31850, x65, SD15/148.5 m. F, top view of QMF 31851, x90, SD210/87.7 m.
G,H, arthrodire indet. infragnathal fragment, G, lingual, H, labial views of QMF 31852, x30, SD198/67.6 m.
I, placoderm indet., crown view of scale QMF 31855, x55, SD238/227 m.
J, arthrodire indet., crown view of scale QMF 31853, x60, SD170/200 m.
K, L, placoderm indet. K, lateral view x30, L, crown view x35 of scale QMF 31854, SD128/130.8 m.
M,N, thelodont indet. M, crown view, N, basal view of scale QMF 31856, x60, SAG/26.8 m.
O,P, ?ptyctodontid indet. quadrate, QMF 31857, x20, SD15/145.6 m.

shallow groove runs parallel to the dorsal margin (Figure 6H); on the other lateral surface a narrow lengthwise ledge is found in the same position (Figure 6G). The posterior part of the bone is broken (Figure 6G).

The scale QMF 31853 (Figure 6J) measures 1mm across the greatest diameter, with a gently convex base and no discrete neck. The ornament consists of a central area of low, broad, closely-packed tubercles gently tapering to a rounded point at the top, with a subcircular cross-section, and up to ten irregularly radiating, sometimes bifurcating, ridges, and small, indistinct nodes on the margins of the scale.

Discussion

Young (1993) mentions the presence in the Broken River Formation of large eubranchyothoracid arthrodires, such as the homostiid *Atlantidosteus*. However, homostiids have a different type of infragnathal from that described here (G C Young, pers. comm.).

Infragnathals have been described from other Australian arthrodires, all eubranchyothoracids: *Goodradigbeeon australianum* from the Early Devonian Taemas Formation at Taemas and Wee Jasper, NSW (White 1978), and from the Frasnian Gogo Formation in WA *Harrytoombsia elegans*, *Camuropiscis concinnus*, *Rolfosteus canningensis*, *Tubonassus lennardsensis*, *Bruntonichthys multidentis*, *Tubonassus fascidens*, *kendrickichthys cavernosus*, *Incisoscutum ritchiei* and *Latocamurus coulthardi* (Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1980, 1981; Long 1988). While the Broken River specimen does not strongly resemble any one of these published forms, it does have some common characters.

Arthrodire infragnathals consist of two main regions – the anterior biting region, usually occupying approximately half the total length of the bone, and commonly bearing one or more rows of teeth, and a posterior expanded blade (Miles and Westoll 1968; White 1978; Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1980, 1981). This specimen is interpreted as part of the anterior biting region of the infragnathal, with the posterior blade missing. It possesses, in common with other described specimens, the deep ventral longitudinal groove for meckels cartilage, a shallow groove on the lateral surface, and denticles or teeth in the biting region. The Broken River specimen differs from previously described specimens in the anterior region, the position of the shallow lateral groove, and the shape and position of the denticles.

The deep ventral groove, found in the Broken River specimen, is commonly, but not always, present in arthrodire infragnathals. A ventral groove for the mentomeckelian bone has been described in *Goodradigbeeon* (White 1978),

Bruntonichthys, *Bullerichthys* and *Kendrickichthys* (Dennis and Miles 1980), and in Northern Hemisphere arthrodires *Coccosteus cuspidatus*, *Dunkleosteus*, *Titanichthys*, *Malerosteus* and some arctolepids, from the Middle Old Red Sandstone of Scotland (Miles and Westoll 1968).

The shallow lateral groove extends to the anterodorsal edge of the specimen (Figure 6H). A similar shallow groove, on the mesial surface and interpreted as the possible path of the ramus mandibularis internus VII, is reported in infragnathals of *Coccosteus*, *Harrytoombsia*, *Camuropiscis*, *Rolfosteus* and *Incisoscutum* (Miles and Westoll 1968; Miles and Dennis 1979; Dennis and Miles 1979a, 1979b, 1981), but occurring only on the posterior blade region parallel to the ventral margin, not on the anterior biting region as in the Broken River specimen. A shallow mesial groove has not been reported in *Goodradigbeeon*, *Bruntonichthys*, *Bullerichthys*, *Kendrickichthys* or *Latocamurus* (White 1978; Dennis and Miles 1980; Long 1988).

The nature of teeth on the biting region varies, and in some genera is difficult to determine as a result of the amount of wear caused by either the anterior or posterior supragathal, or both (e.g. Dennis and Miles 1980). *Camuropiscis*, *Bruntonichthys* and *Incisoscutum*, for example, have two dorsal or mesial rows of teeth and a short anterior row of symphyseal teeth (Dennis and Miles 1979a, 1980, 1981). The unworn part of the dorsal tooth row in *Bullerichthys* comprises ten pointed, forward-facing teeth, smallest posteriorly (Dennis and Miles 1980). *Tubonassus*, in contrast, has shearing edges on the infragnathal rather than a biting surface with teeth (Dennis and Miles 1979b), while *Goodradigbeeon* has no apparent teeth or cutting edges (White 1978).

The spatulate denticles on the dorsal edge of the Broken River specimen differ from these other arthrodires. The biting region is not flattened, but the denticles are aligned longitudinally along a narrow dorsal ridge. There are no anterior symphyseal teeth; the anterior extremity of the Broken River infragnathal narrows and extends slightly ventrally, in contrast to the dorsally-curving anterior end of other described infragnathals (e.g. *Camuropiscis* Dennis and Miles 1979a, figure 14a, b; *Bullerichthys* Dennis and Miles 1980, figure 12A, C; *Kendrickichthys* Dennis and Miles 1980, figure 20A, B).

Abundant bichanosteoid-type scales occur in the Emsian Taemas-Buchan fauna (Schultze 1968; Giffin 1980; G.C. Young, pers. comm.), in horizons of a comparable age to those at Broken River where only a single similar specimen was recovered, despite extensive sampling (particularly in section SD170). These two regions, although separated by approximately 2000 km, were both shallow marine

environments situated on the northeastern margin of Gondwana during the Devonian (Scotese and McKerrow 1990), and so could be expected to have similar faunas. Indeed, preliminary studies of microvertebrate faunas from Buchan and Taemas reveal cheiracanthoid and nostolepid scales and onychodontid teeth, not unlike those found at Broken River.

Order Ptyctodontida Gross, 1932

Family Ptyctodontidae Woodward, 1891

?Ptyctodontid indet.

Figures 6B, O, P

Material

One probable supragathal (upper toothplate) fragment (QMF 31847; Figure 6B) and one quadrate (QMF 31857; Figures 6O, P).

Localities

QMF 31847: SD111/29 m; Dosey Limestone.

QMF 31857: SD15/145.6 m; Papilio Formation.

Stratigraphic levels

QMF 31847: Eifelian (*ensensis* Zone).

QMF 31857: Givetian (Middle *varcus* Zone).

Remarks

Specimen QMF 31847 (supragathal) is placed tentatively in the family Ptyctodontidae as it has a wedge-shaped cross-section similar to *Ctenurella gardineri* (and as reported by Watson 1938 in *Rhamphodopsis*) and the anteroventral corner of the biting edge extended into a slight, rounded beak as in *C. gardineri* and *Campbellodus decipiens* (Miles and Young 1977). The Broken River specimen also resembles figured *Rhynchodus*-type supragathals from the Frasnian and Famennian of Iran (Lelièvre *et al.* 1981: figure 23A,B). The broken dorsal edge of the specimen prevents observing the presence of an anterior dorsal process, found in *Ctenurella*, *Campbellodus* and *Rhamphodopsis trispinauts* (Miles 1967; Miles and Young 1977). The mesial surface just behind the anterior margin lacks the grooves common in ptyctodontids (Miles and Young 1977).

Specimen QMF 31857 (quadrate) is also placed tentatively in this family as it is similar to a quadrate of *C. gardineri* (Miles and Young 1977) recovered from the Frasnian Gogo Formation. This specimen differs from *C. gardineri*, however, in lacking the lateral and mesial ridges adjacent to the main shaft of the bone that articulated with the upper toothplate, and in possessing an articular process (arrow in Figure 6P) at the posteroventral end. Indeed, any placoderm group without dermal bones in the cheek (e.g. phyllolepid) could have a quadrate similar to this specimen (G.C. Young, pers. comm.).

Description

QMF 31847: The 2 mm long fragment is incomplete dorsally and posteriorly, with open spongy bone visible along the dorsal margin. The anterior margin is extended ventrally into a slight, rounded beak. The surface is unornamented and shows no evidence of lamellae or grooves.

QMF 31857: This fragment is about 2.5 mm long. The open, flared anterior end (Figure 6O) is hollow for about half the total length of the fragment. The opposite, posteroventral end has a solid, rounded condyle, interpreted as the articulating surface with the articular bone of the mandibular joint, and a separate shallow, hollow cylindrical process (arrow in Figure 6P).

Discussion

Quadrates from several arthrodires from the Frasnian Gogo Formation have been figured and described; none resemble the Broken River specimen. The quadrate of *Camuropiscis* is co-ossified with the palatoquadrate (Dennis and Miles 1979a), and that of *Rolfosteus* and *Kendrickichthys* with the postsuborbital plate (Dennis and Miles 1979b, 1980). In *Incisoscutum* and *Latocamurus* the quadrate is a separate, elongate bone (Dennis and Miles 1981; Long 1988).

Ptyctodontids had a pair of upper and lower toothplates that operated by crushing, grinding or shearing (Denison 1978). *Ctenurella*, *Campbellodus* and *Rhamphodopsis* have a shearing edge on the lingual surface (Miles 1967; Miles and Young 1977), whereas the biting areas of *Ptyctodus* and *Palaeomylus* bear tritons and rounded tritoral cusps, respectively (Ørvig 1960). The family has been reported from the Early Devonian of Iran and the Soviet Arctic, the Emsian Taemas–Buchan fauna of southeastern Australia, and the Eifelian to Famennian of North America, Europe, Scotland, former USSR, Iran, Libya and Australia (Hussakof and Bryant 1918; Ørvig 1960; Miles 1967; Miles and Young 1977; Denison 1978; Lelièvre *et al.* 1981, 1988).

Placoderm indet.

Figures 6I, K, L

Material

Three scales (QMF 31854,5 and one other).

Localities

SD128/137 m and SD238/227 m; Papilio Formation.

Stratigraphic level

Givetian (*varcus* Zone).

Description

The figured scales measure 1.1–1.2 mm along the

greatest diameter, and have a gently convex or flat base. The crown ornament consists of a central area of posteriorly-inclined, pointed, stellate tubercles. In one specimen (Figure 6K, L), the tubercles are closely-packed, with larger ones in the centre; in the other figured specimen (Figure 6I) the tubercles are more widely spaced. In both specimens the central tuberculated region of the crown is surrounded by a marginal area of small rounded nodes in concentric rows.

Discussion

Similar scales are figured by Obruchev and Karatajute-Talimaa (1967, plate 1, figure 9), assigned to a rhenanid related to *Radotina* from the Early Devonian of eastern Europe; by Goujet (1976, plate 62, figures 12 and 14), assigned to an indeterminate radotinid from the Lochkovian-Pragian of France; and mentioned by Turner and Murphy (1988) from the Pragian Martin's Well Limestone at Broken River and from the Early Devonian of NSW.

Class Teleostomi

Subclass Osteichthyes Huxley, 1880

Infraclass Crossopterygii Huxley, 1861

Order Struniiformes Jessen, 1966

Family Onychodontidae Woodward, 1891

Onychodontid indet.

Figures 5A–G

Material

430 whole or parts of teeth (QMF 31834–5 and 428 others; Figures 5A, B); Two scale fragments (QMF 31836–7; Figures 5C, D); Eight tooth-bearing bone fragments (QMF 31838–9 and six others; Figures 5E–G).

Localities

QMF 31834–5: SD15/14.2–213.8 m, SD111/31–240 m, SD128/54.3–201.5 m, SD130/3.6–63.5 m, SD131/92.1–207.4 m, SD146/429.5 m, SD164/80.8–124.1 m, SD170/200–850 m, SD192/0–60 m, SD198/111.9 m, SD204/95–120 m, SD210/69.7–104 m, SD216/0–107 m, SAG/16.1–112 m and SAGW/17.1–20 m; Papilio and Bracteata formations, Lomandra, Dosey, Spanner, Stanley and Chinaman Creek limestones.

QMF 31836–7: SD164/24.7 m; Papilio Formation.

QMF 31838–9: SD15/107.9 m, SD128/104.2–118.8 m, SD204/114.2–115.9 m, SD210/87.7 m and SD216/29.2 m; Papilio Formation and Spanner Limestone.

Stratigraphic ranges

QMF 31834–5: Emsian (*serotinus* Zone) to earliest Frasnian (*asymmetricus* Zone).

QMF 31836–7: Givetian (Upper *varcus* Zone).

QMF 31838–9: Givetian (Lower and Middle *varcus* zones).

Remarks

The teeth are compatible with the description by Wells (1944:44) of the prearticular and coronoid series set in the jawbone between the longer, more slender dentary teeth.

The scale fragments resemble the *Onychodus* scales discussed and figured by Wells (1944:44, figure 9c). Scales with ornament of horseshoe-shaped denticles with a flattened or slightly concave top face have also been described or figured in the literature from porolepiforms and dipnoans: on scales of the porolepiforms *Heimenia ensis* Ørvig 1969 (figure 6D) and *Porolepis* (Ørvig 1957, figure 8C) along the anterior border, and *Laccognathus* and *Glyptolepis* (Ørvig 1957, figures 2B, 4C, 10B) on the overlapped portion; scales of the onychodontid *Onychodus* (Ørvig 1957, figures 7C, E); and the dipnoan *lowadipterus halli* Schultze, 1992 (figure 9A). However, in none of these scales are the horseshoe-shaped tubercles interspersed with smaller, rounded tubercles arranged linearly, as in the Broken River specimens.

The tooth-bearing bone fragments resemble those of *Onychodus* sp. (e.g. Wells 1944, plate 3, figure 37; Vieth-Schreiner 1983, plate 4, figures 44–45), and are socketed in the jawbone. However, these teeth are smooth, in contrast to the striated teeth of *Onychodus*.

Description

QMF 31834–5: The teeth are slender, conical and curved with fine longitudinal striations; the striations cover the whole surface of the cusp, unlike the chondrichthyan phoeodont cusp discussed above, with striations only on the labial surface. Length ranges from 0.5 mm to approximately 2.5 mm. The base of most specimens is tapering and nonfluted.

QMF 31836–7: Surface ornament is of coarser horseshoe-shaped, flattened denticles about 100 µm long and 50 µm high, interspersed with rows of finer tubercles (Figure 5C). The base of the scale fragments is flat and unornamented.

QMF 31838–9: The fragments are up to about 2 mm long, with smooth, conical, socketed teeth up to about 0.5 mm long. Broken cusps show a central pulp cavity (Figures 5F, G).

Discussion

A specimen from the Emsian *Spirifer yassensis* Limestone of the Murrumbidgee area, NSW, described by Ørvig (1969, figure 11c) as a premaxillary of a struniiform crossopterygian, has conical, socketed teeth with a central pulp cavity,

as found in the Broken River specimens (Figures 5F, G). Similar specimens are currently emerging from acid-leaching of material from Fish Hill, a limestone outcrop approximately 10 km northeast of SD216 (S. Turner, pers. comm.).

Onychodus sp. has been reported from the Early to Late Devonian of Australia, North America, Europe and the Middle East (Wells 1944; Blicek *et al.* 1980; Giffin 1980; Vieth-Schreiner 1983; Lelièvre *et al.* 1988; Turner and Murphy 1988). The distinctive conical, finely striated teeth of onychodontids are common in Australian microvertebrate residues throughout the Devonian (S. Turner, pers. comm.).

Infraclass Dipnoi Muller 1844

?Dipnoan indet.

Figures 5O, P

Material

One probable dipnoan toothplate (QMF 31845).

Locality

SD131/117.7 m; Papilio Formation.

Stratigraphic level

Givetian (Middle *varcus* Zone).

Description

The specimen is about 1.5 mm long, and has radiating rows of rounded conical denticles that increase in size towards the outer edge of the plate. The anterior edge of the fragment (to the bottom in Figure 5O) has closely-packed, smaller denticles. The underside is slightly concave, unornamented, and appears to be slightly rougher in texture than the smooth denticles. Possibly the specimen has split from the underlying bone along a basal pulp cavity, so that the base of the toothplate is missing.

Discussion

Three types of lungfish are known from Fish Hill at Broken River, approximately 10 km northeast of the present study area (S. Turner, pers. comm.).

Cosmine scales

Figures 5H–J

Material

Six scales or fragments (QMF 31840–2 and three others).

Localities

SD15/145.6–148.5 m, SD170/483 m, SD204/120 m, SD210/87.7 m, SD216/48.5 m; Papilio Formation, Lomandra and Spanner limestones.

Stratigraphic range

Eifelian (*costatus* Zone) and Givetian (Middle *varcus* Zone).

Remarks

Cosmine, a hard tissue composed of enamel plus dentine and perforated by pores, formed the surface layer of scales of Devonian crossopterygians and dipnoans.

Description

The scales have a shiny, coarsely porous surface layer. The pores are of similar size, fairly closely-packed, and regularly arranged (Figures 5H, I). The pores may open obliquely within semi-elliptical depressions (e.g. Figures 5L, J), or directly to the surface (Figure 5H).

Discussion

One scale (Figure 5H) has a square base with a deep, wide groove running across the scale, and is much deeper than the others. It resembles lepidotrichia of the dipnoan *Dipterus* described and illustrated by Campbell and Barwick (1988, figures 29C, 30, 31A, B, C).

The semi-elliptical depressions in the cosmine have been illustrated in porolepiform rhipidistians (e.g. Schultze 1977, plate 13, figure 1a) but are absent in dipnoans, although this distinction may not be apparent in Early Devonian forms (V. Karatajute-Talimaa, pers. comm., 1994; E. Mark-Kurik, pers. comm., 1994). This generalisation may not apply in all cases, however, since porolepiforms and dipnoans are closely related (Chang and Smith 1992).

Infraclass Actinopterygii

Order Palaeonisciformes Hay, 1929

Palaeoniscoid indet.

Figures 6A, C–F

Material

One scale (QMF 31846) and 34 tooth-bearing plates (QMF 31848–51 and 30 others).

Localities

QMF 31836: SD192/60 m; Stanley Limestone.
QMF 31848–51: SD15/148.5 m, SD128/78.2–196.6 m, SD130/73.6–143 m, SD131/92.1 m, SD204/95–120 m, SD210/87.7 m, SD216/30.3 m and SAG/117.7 m; Papilio Formation, Spanner and Chinaman Creek limestones.

Stratigraphic range

QMF 31836: Earliest Frasnian (*asymmetricus* Zone).

QMF 31848–51: Eifelian (*ensensis* Zone) to Givetian (Upper *varcus* Zone), with one specimen from a horizon older than *ensensis* Zone.

Remarks

The Broken River scale is a similar shape to those of *?Moythomasia* sp. figured by Storrs (1987, figures 5.1 and 5.2) from the Givetian to Frasnian of Iowa, although these scales lack the surface holes of the Broken River specimen. Two scales figured by Liszkowski and Racki (1992, figures 9F and 9I), described respectively as *Moythomasia* (?) sp. and undetermined palaeoniscoid, resemble the Broken River scale in general morphology.

Description

The slightly broken, abraded scale measures almost 2 mm in length. It is thin and flat, and ornamented with rows of irregularly spaced canal pores. These rows of pores lie between the ganoine ridges (Janvier 1974). The area of overlap by adjacent scale(s) is smooth (Stamberg 1988). There is evidence of a series of parallel ridges, now worn, alongside the anterior margin. The posterior edge extends into short, broad denticles (Figure 6A).

The thin, conical teeth are attached to plates or bases (Figures 6C–F). The cusps range in length up to about 0.6 mm. The bases are generally thin and flat, and appear to consist of a less dense, bone-like tissue in contrast with the smooth, dense cusp material. Very few specimens have the acrodin tip still intact; in these, the delineation between the opaque enamel-coated main part of the tooth and the transparent tip is clearly marked.

Discussion

Moythomasia sp. is described as a whole specimen from the late Middle and early Late Devonian of Germany (Gross 1953) and the Frasnian Gogo Formation of WA (Gardiner 1984), and reported from Late Devonian unspecified horizons at Pandanus Creek, Broken River, Queensland (Long and Turner 1984), the Givetian of France (Lelièvre *et al.* 1986), and the Late Devonian of Iran (Bartram 1981). The Broken River scale differs in shape and ornament from other Early and Middle Devonian palaeoniscoid scales from eastern Australia, such as *Ligulepis toombsi* (Schultze 1968; Giffin 1980) and indeterminate palaeoniscoid scales (Giffin 1980, figure 11) from the Early Devonian Taemas Formation.

The Broken River scale lacks the peg and socket articulation so it may have come from the area near the tail of the fish (Area D in Esin 1990, figure 2). In such scales the length exceeds the height, the peg and socket articulation is absent, and sculpture on the free field area of the scale is minimal (Esin 1990). Also, the Broken River scale has a similar rhombic shape to the *Amblypteria costata*

(Eichwald) scale from Area D near the tail, figured by Esin (1990, plate VIII, figure 1).

?Osteichthyan indet.

Figures 5K–N

Material

Fifteen toothplate fragments (QMF 31843,4 and thirteen others).

Localities

SD15/66 m, SD128/78.2–188.4 m, SD131/117.7–208.3 m, SD164/24.7–117.7 m, SD204/115.9–120 m and SD216/96.2 m; Papilio Formation and Spanner Limestone.

Stratigraphic range

Givetian (Lower *varcus* to *hermanni-cristatus* Zones).

Description

The fragments range up to about 2 mm long. The top is covered by closely-packed, blunt spatulate denticles (Figures 5L,M); the longer side of these denticles is parallel to the longer edge of the fragments. The denticles are up to 0.3 mm high, and have a central pulp cavity (arrow in Figure 5L). The bony base has a wide shallow longitudinal groove on the underside, and its surface appears slightly porous and less dense than the surface of the unornamented denticles.

ACKNOWLEDGEMENTS

I am indebted to Ruth Mawson and John Talent for supplying their material for study, and for giving valuable advice, support and encouragement at all stages of the project. Special thanks to Gavin Young and Sue Turner, who have given helpful advice and assistance with identification over a prolonged period; Glenn Brock for preparing Figure 2; and Michael Engelbreetsen, Coral Gilkeson and Annabelle Gregor for assistance with SEM photography. I thank Philippe Janvier, Jo Vergoossen, John Long, Anne Kemp, Carole Burrow, Jennifer Clack, Ross Parkes and Mark Hocking for useful discussion and suggestions regarding identification, Dianne Hughes for discussion of thin sections and use of her photographic equipment, Theresa Winchester-Seeto for helpful advice and encouragement, and Ken Rousell for drafting Figure 1. Thanks to Gavin Young, John Long, Sue Turner and an anonymous referee for suggesting improvements to earlier drafts of the manuscript. I am grateful to the Australian IGCP committee for awarding a Grant-in-Aid as financial assistance towards participation at the Premiers Vertébrés et Vertébrés Inférieurs

conference, Paris. This paper is a contribution to IGCP 328.

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Manuscript received 3 May 1995; accepted 7 November 1995.

A new species of Cardinalfishes (Apogonidae) from northern Australia

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Abstract – A new species of apogonid fish is described on the basis of five trawl-captured specimens from northwestern Australia. *A. fuscomaculatus*, sp. nov. appears to be most closely related to *A. striatus* from the Indo-Malay Archipelago. The two species have similar low gill raker counts (8–9 developed rakers), fin shapes (relatively low dorsal and anal with slightly rounded caudal), and preopercle serration (moderate serrae on margin and smooth ridge). Additionally, they both possess a silvery abdomen and a similar pattern of three dark lines radiating from the eye. They differ markedly, however in overall colour pattern. *A. fuscomaculatus*, sp. nov. has large dark spots on the side of the body compared with about 10 narrow bars on the side of *A. striatus*.

INTRODUCTION

The fishes of the family Apogonidae, popularly known as cardinalfishes, are common reef inhabitants of tropical and subtropical regions. They are relatively small (rarely exceeding 10 cm in standard length), often brightly coloured fishes, with two separate dorsal fins (the first of six to eight spines), and a large oblique mouth. Most seek shelter during the day, emerging at night to feed on small benthic invertebrates (primarily crustaceans). They are oral-brooders, the males holding the fertilised ova in their mouth for several days until hatching. The family is large, estimated to contain 250 species in 21 genera. The present paper describes a new species of *Apogon* Lacepède collected by trawl in relatively deep water off north-western Australia.

Type specimens have been deposited in the Museum and Art Gallery of the Northern Territory, Darwin (NTM) and the Western Australian Museum, Perth (WAM).

Lengths given for specimens are standard length (SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of hypural plate); body depth is the maximum depth from the base of the dorsal spines; body width is measured just posterior to the gill opening; head length is taken from the front of the upper lip to the end of the opercular membrane, and snout length from the same anterior point to the fleshy edge of the orbit; orbit diameter is the greatest fleshy diameter, and interorbital width the least bony width; caudal peduncle depth is the least depth, and caudal peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and soft rays are measured to their extreme bases.

Pectoral-ray counts include the upper rudimentary ray; lateral-line scale counts are made to the base of the caudal fin (hence do not include the pored scales posterior to the hypural plate); gill-raker counts are made on the first gill arch and include developed rakers only (those which are higher than the width of their base); the count of the upper-limb rakers is given first, followed by the lower-limb count; the raker at the angle is contained in the lower-limb count.

Proportional measurements of type specimens are given in Table 1 as percentages of the standard length. Data in parentheses in the description refer to paratypes.

SYSTEMATICS

Apogon fuscomaculatus, sp. nov.

Figure 1; Table 1

Holotype

NTM S.13284–014, 48.5 mm SL, NE of Charles Point, Darwin, Northern Territory, (approximately 12°17'S, 130°40'E), 18–24 m, trawl, R. Williams, 2 September 1992.

Paratypes

NTM S.11672–027, 51.1 mm SL, S of Rowley Shoals, Western Australia (approximately 19°02'S, 118°30'E), 82–86 m, trawl, NT Fisheries Dept., 2 June 1985; NTM S.11673–037, 43.7 mm SL, S of Rowley Shoals, Western Australia (approximately 19°12'S, 118°41'E), 76–80 m, trawl, NT Fisheries Dept., 1 June 1985; NTM S.13337–003, 45.0 mm SL, SW of Flat Top Bank, Timor Sea (approximately 19°02'S, 118°30'E), 82–86 m, trawl, NT Fisheries Dept., 23 November 1990; WAM P.30992–001, 48.5 mm SL, same data as NTM S.11673–037.

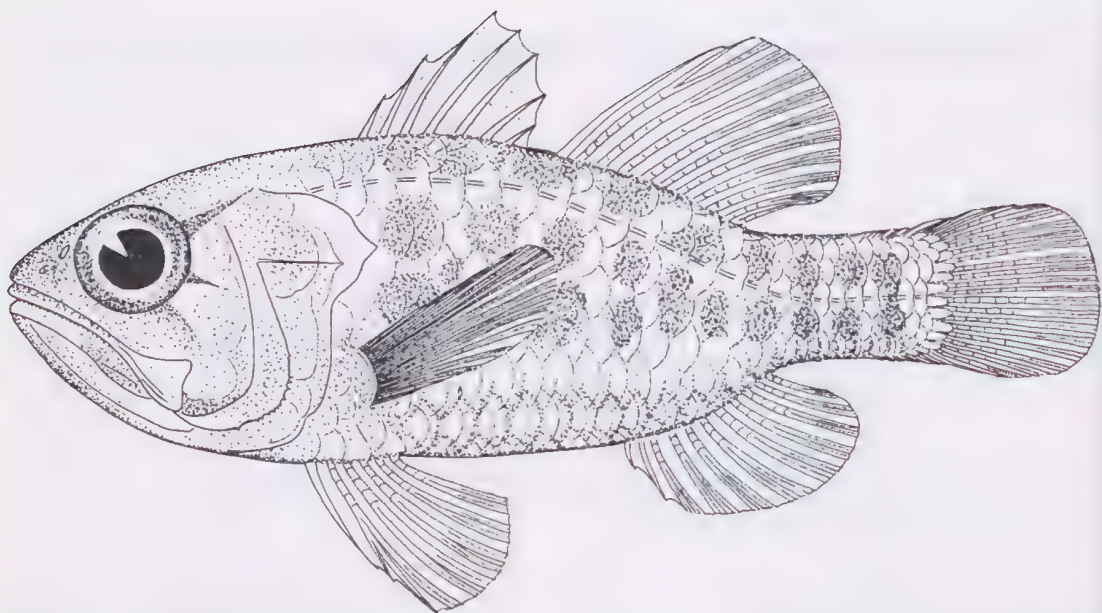


Figure 1 *Apogon fuscomaculatus*, holotype, 48.5 mm SL. Damaged scales and fins have been reconstructed. Drawing by S. Morrison.

Diagnosis

Dorsal rays VII–I,9; anal rays II,8; pectoral rays 15–16; lateral-line scales 24; predorsal scales 2–3; developed gill rakers 8–9; preopercular margin serrate; preopercular ridge smooth; body depth 2.9–3.5 in SL; overall colour pale with 3–4 horizontal rows of large brown spots on side, belly silvery, 3 narrow lines radiating from rear half of eye, and fins pale to dusky.

Description

Dorsal rays VII–I,9; anal rays II,8; all dorsal and anal soft rays branched, the last to base; pectoral rays 15 (one paratype with 16), lowermost and two uppermost unbranched; pelvic rays I,5, all rays branched; principal caudal rays 17, upper and lower rays unbranched; upper and lower procurent caudal rays 7, posteriormost (and occasionally that preceding it) segmented; lateral-line scales 24, plus 4 pored scales posterior to hypural plate, the last (missing on all but one paratype) long and narrow, somewhat triangular; scales above lateral line to origin of dorsal fin 2; scales below lateral line to origin of anal fin 6; median predorsal scales about 2–3 (scales missing on most specimens; circumpeduncular scales 12; developed gill rakers 1 + 8 (1+7–8); branchiostegal rays 7; supraneural (predorsal) bones 3; vertebrae 10 + 14.

Body depth 2.9 (2.9–3.5) in SL; body width 1.8 (2.0–2.3) in depth; head length 2.3 (2.2–2.5) in SL; dorsal profile of head straight except for rounded

front of snout; snout length 4.1 (3.9–4.7) in head; orbit diameter 3.2 (3.0–3.4) in head; interorbital width 3.8 (3.8–4.1) in head; caudal peduncle depth 2.7 (2.7–3.2) in head; caudal peduncle length 2.5 (2.2–2.8) in head.

Mouth large, the maxilla reaching vertical at rear edge of pupil or beyond this point, upper jaw length 2.0 (1.8–2.0) in head; mouth oblique, gape forming an angle of about 30 degrees to horizontal axis of head and body; posterior edge of maxilla slightly concave; no supramaxilla present; lower jaw slightly inferior; upper and lower jaws with a band of small villiform teeth in five to six irregular rows; irregular row of small teeth forming a “V” on vomer; double row of small conical teeth on palatines. Tongue broad-based with rounded tip.

Anterior nostril a small, low-rimmed, membranous tube directly in front of center of eye about half distance from edge of orbit to front of upper lip; posterior nostril ovate without a rim, on a line connecting anterior nostril to top of orbit, more than twice as large as anterior nostril. Cephalic lateralis pores numerous, especially on interorbital, around eye, and on ventral surface of lower jaw.

A single, flat, obtuse opercular spine. Preopercular margin serrate (21 serrae on left side of holotype and 13–16 on paratypes); preopercular ridge smooth.

Scales weakly ctenoid. Lateral line conspicuous, nearly paralleling dorsal contour of body, and ending short distance posterior to caudal-fin base

Table 1 Proportional measurements of type specimens of *Apogon fuscomaculatus* expressed as percentage of the standard length.

Character	Holotype NTM S.13284 -014	Paratype NTM S.11672 -027	Paratype WAM P.30992 -001	Paratype NTM S.13337 -003	Paratype NTM S.11673 -037
Standard length (mm)	48.5	51.1	48.5	45.0	43.7
Body depth	35.1	32.1	34.8	34.9	28.4
Body width	19.6	14.1	16.1	15.8	14.4
Head length	43.5	39.3	45.4	44.2	42.3
Snout length	10.5	10.0	10.3	10.9	8.9
Orbit diameter	13.6	13.1	13.2	12.9	14.0
Interorbital width	11.3	10.4	11.3	11.1	10.3
Upper jaw length	21.9	21.5	22.9	22.0	21.1
Caudal peduncle depth	15.9	14.5	14.0	15.8	13.5
Caudal peduncle length	17.7	18.0	17.5	16.0	15.3
Predorsal length	43.9	45.2	47.0	40.7	44.4
Preanal length	71.8	71.8	75.1	72.2	74.1
Prepelvic length	39.2	38.6	38.1	38.9	39.6
Length 1st dorsal spine	4.5	4.5	3.7	4.9	3.9
Length 2nd dorsal spine	10.1	10.0	7.8	10.2	8.2
Length 3rd dorsal spine	17.3	16.4	14.2*	10.7*	15.6
Spine of 2nd dorsal fin	13.0	13.2	13.2	13.2	13.2
Longest soft dorsal ray	23.1	22.1	18.8	23.1	22.4
Length 1st anal spine	2.9	3.7	3.3	3.1	3.7
Length second anal spine	10.3	10.2	11.1	11.3	10.1
Longest anal soft ray	19.8	18.4	17.7	19.3	20.1
Caudal fin length	27.0	29.2	27.4	25.6	27.2
Pectoral fin length	21.9	19.6	20.2	22.4	20.1
Pelvic spine length	13.4	11.4	11.5	12.9	12.4
Pelvic fin length	23.9	22.1	22.1	23.6	23.8

* indicates damaged condition

(four pored scales posterior to hypural, the last pointed). No scales on dorsal and anal fins except low sheath at base of second dorsal and anal fins; small scales on basal third of caudal fin; no scales on paired fins except pair of large midventral scales at base of pelvic fins.

Origin of first dorsal fin above third lateral-line scale; first dorsal spine slender and short, 9.6 (8.7–12.2) in head; third dorsal spine longest, 2.5 (2.4–4.1) in head; middle soft dorsal rays longest, 1.9 (1.8–2.4) in head; origin of anal fin below base of third dorsal soft ray; first anal spine very short, 15.1 (10.6–14.2) in head; second anal spine 4.2 (3.9–4.2) in head; middle anal soft rays longest, 2.2 (2.1–2.6) in head; caudal fin slightly rounded, 1.6 (1.3–1.7) in head; middle pectoral rays longest, 2.0 (2.0–2.2) in head; origin of pelvic fins slightly anterior to pectoral-fin base; first pelvic soft ray longest, reaching to about anus, its length 1.8 (1.8–2.1) in head.

Colour in alcohol: Overall pale tan, nearly white, with 3–4 horizontal rows of large (largest are nearly size of pupil), irregular brown spots on side of body; abdomen slightly silvery; a pair of faint brownish, diagonal lines radiating from rear margin of eye across upper preoperculum; a

similar, slightly wider band from lower edge of eye across cheek; fins whitish, except for fine pepper-like pigmentation most heavily concentrated on membranes of first dorsal fin, outer edge of anal fin and along anterior edge of pelvic fins. Colour in life is unknown.

Remarks

Apogon fuscomaculatus has been collected from the vicinity of Darwin, Northern Territory and on the outer edge of the North West Shelf of Western Australia. It apparently inhabits flat sand or rubble bottoms, probably sheltering among gorgonians and sponges. Depth of collection ranged between 18–86 m, which is relatively deep compared to the shallow range (less than 20 m) for most members of the family.

A. fuscomaculatus belongs to the subgenus *Nectamia* Jordan, as defined by Fraser (1972); however, this name is now replaced by *Ostorhinchus* Lacepède (Randall *et al.* 1990). This subgenus is by far the largest within *Apogon*, containing at least 60 species. *A. fuscomaculatus* appears to be closely related to *A. striatus* (Smith and Radcliffe 1912) from the Indo-Malay Archipelago. The two species have similar low gill

raker counts (8–9 developed rakers), fin shapes (relatively low dorsal and anal with slightly rounded caudal), and preopercle serration (moderate serrae on margin and smooth ridge). Furthermore, they both possess a silvery abdomen and a similar pattern of three dark lines radiating from the eye. They differ markedly, however, in overall colour pattern. *A. fuscomaculatus* has large dark spots on the side of the body compared to about 10 narrow bars on the side of *A. striatus*. *Apogon melanopus* (Weber 1911) of north-western Australia and the Aru Islands and *A. fuscomaculatus* exhibit similar patterns of large spots on the side of the body, but the former species differs in having a dark bar below the first dorsal fin, intensely black pelvic fins, serrae on the preopercular ridge, at least 14 developed gill rakers on the first arch, and an emarginate caudal fin. *Apogon fusovatus* Allen (1985) is a junior synonym of *A. melanopus*.

The species is named *fuscomaculatus* (Latin: "dusky-spotted") in reference to the dominant colour pattern feature.

ACKNOWLEDGEMENTS

We thank Helen Larson and Rex Williams of

NTM for informing us of the existence of this species and providing loan material.

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Manuscript received 29 May 1995; accepted 18 December 1995.

Two new species of the water mite genus *Penemideopsis* from Western Australia (Acarina: Mideopsidae)

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Abstract – *Penemideopsis pusilla* sp. nov. and *P. angovens* sp. nov. are each described from single males collected in southwestern Australia, and compared with *P. phreatica* from Victoria.

INTRODUCTION

The genus *Penemideopsis* was described by Cook (1986) from a single male specimen collected from interstitial deposits in eastern Victoria. This species, *P. phreatica* Cook, differed from all other mideopsids by the combined presence of a greatly enlarged tubercle and seta on the pedipalpal tibia, the possession of only three pairs of acetabula, and lobes covering the openings of leg IV (Cook 1986). The discovery of two additional specimens of *Penemideopsis* amongst collections from Western Australia made available by Dr Jenny Davis (Murdoch University) and Dr Stuart Halse (Department of Conservation and Land Management) has significantly expanded the geographic distribution of the genus, and these species differ in small but significant ways from the type species. The Western Australian specimens are described here and compared with *P. phreatica*.

These two new species of *Penemideopsis* represent the second genus of small, presumably interstitial, mideopsid reported from Western Australia. Like each of the species described here, the first, *Tillia davisae* Harvey, has been collected only once (Harvey 1990).

The specimens are mounted on microscope slides in glycerol gel or Hoyers mountant, and lodged in the Western Australian Museum, Perth (WAM). Nomenclature of the leg segments follows Harvey (1996).

SYSTEMATICS

Family Mideopsidae Koenike

Genus *Penemideopsis* Cook

Penemideopsis Cook, 1986: 300.

Type species

Penemideopsis phreatica Cook, 1986, by original designation.

Diagnosis

Male (modified from Cook 1986)

Pedipalp not uncate; tibia with greatly enlarged ventral seta set in large tubercle. Medial margins of coxa IV broad; projections covering openings of leg IV either greatly enlarged or small. Swimming setae absent. Males without any pronounced modifications of the legs, presumably indicating a lack of sexual dimorphism. Three pairs of acetabula; gonopore narrow, but bulging outwards in the region of the first two pairs of acetabula.

Remarks

The discovery of two additional species of *Penemideopsis* requires a slight alteration to the generic diagnosis, as the projections covering the openings of coxa IV range from large (*P. phreatica*) to small (*P. pusilla* and *P. angovens*).

Key to species of *Penemideopsis* (males only)

- Projections covering openings of coxa IV large; outer coxal margins distinctly bulging
..... *Penemideopsis phreatica* Cook
Projections covering openings of coxa IV small (Figures 2, 8); outer coxal margins smooth (Figures 2, 8) 2
- Dorsoglandularial setae situated close to glandularia (Figure 1); posterior margin of coxa IV extending past anterior margin of genital field (Figure 2)
..... *Penemideopsis pusilla* sp. nov.
Dorsoglandularial setae situated far mesal to glandularia (Figure 7); posterior margin of coxa IV not reaching anterior margin of genital field (Figure 8)
..... *Penemideopsis angovens* sp. nov.

Penemideopsis pusilla sp. nov.

Figures 1–6

Material Examined

Holotype

♂, Gooralong Brook, west end of Jarrahdale, Western Australia, Australia, 32°20'S, 116°03'E, 17 June 1986, M. DeHaan (WAM 95/772).

Diagnosis

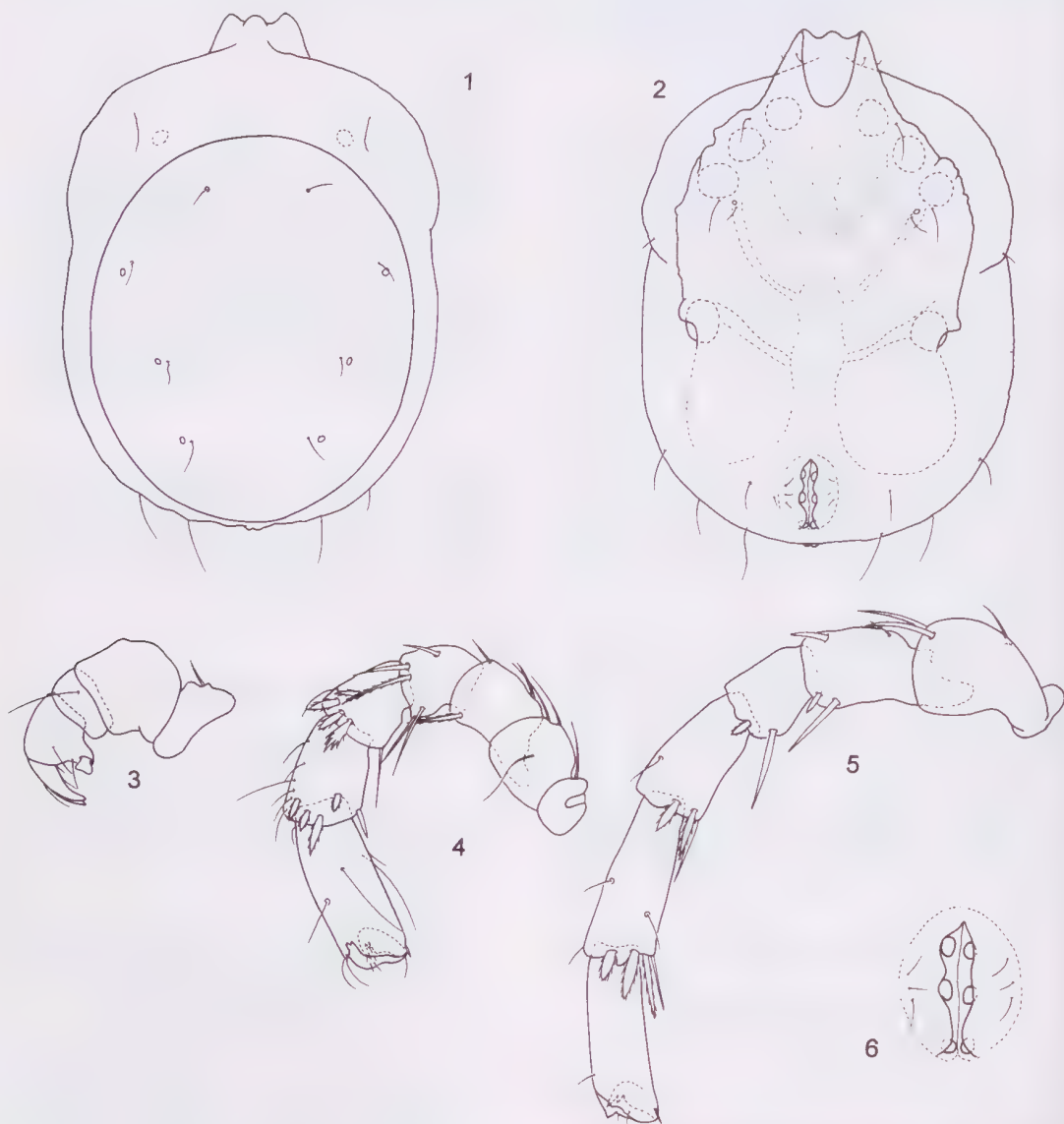
Penemideopsis pusilla differs from *P. phreatica* as follows: projections covering openings of leg IV not greatly enlarged (Figure 2); capitular bay projecting far forward of ventral shield (Figure 2); outer coxal

margins not protruding (Figure 2); and its smaller size (e.g. dorsal shield 339 µm in *P. pusilla*, 395 µm in *P. phreatica*). It differs from *P. angovens* by the dorsoglandularial setae being situated close to the glandularia (Figure 1). It differs from both species by the posterior margin of coxa IV extending well past the anterior margin of the genital field (Figure 2)

Description

Male

Dorsal and ventral shields present. Lateral eyes present; medial eye present, but very small (Figure 1). Dorsal shield (Figure 1) entire and ovoid, widest



Figures 1–6 *Penemideopsis pusilla* sp. nov., holotype ♂: 1, dorsal shield; 2, ventral shield; 3, right pedipalp; 4, right leg III; 5, right leg IV; 6, genital field.

medially; bearing 3 pairs of sub-equidistant dorsoglandularia; dorsoglandularial setae situated close to glandularia; postocularia well anterior to anterior-most glandularia of dorsal shield. Ventral shield (Figure 2) entire; vg1 situated near posterior margin of coxa II; all coxal suture lines visible, those between I and II, II and III, and III and IV posterior-laterally directed, thus forming acute angles with mid-line; medial margin of coxa IV broad; posterior margin of coxa IV rounded, extending past anterior margin of genital field; outer coxal margins not protruding; openings of leg IV covered by small ventral lobes; capitular bay deep and basally rounded, extending far forward of ventral shield; excretory pore incorporated into ventral shield. Genital field (Figure 6) with 3 pairs of small acetabula situated within field. Capitulum and chelicera basically as for *P. phreatica* (Cook 1986: figure 1611). Pedipalp (Figure 4) not uncate; tibia with large ventral projection bearing greatly enlarged spatulate seta; all setae acuminate. Legs (Figures 5, 6) not modified and without swimming setae; with very few serrate setae; claws with ventral clawlets.

Dimensions (μm) ♂: dorsal shield 339/268, ventral shield 429/305. Pedipalp: trochanter 24, femur 45, patella 18, tibia 29, tarsus 31. Leg I: trochanter 52, femur 40, patella 35, tibia 40, metatarsus 50, tarsus 81. Leg IV: trochanter 64, femur 56, patella 43, tibia 60, metatarsus 79, tarsus 75.

Remarks

Despite several visits to the type locality, this species has not been recollected, and appears to be extremely rare. Davis *et al.* (1988) report that the type locality (site C) is amidst jarrah forest and urban development, and that the riparian vegetation is patchy.

Etymology

The specific epithet refers to the small size of the holotype (*pusilla* Latin, very little).

Penemideopsis angovensensis sp. nov.

Figures 7–11

Material Examined

Holotype

♂, Angove River, north of Two Peoples Bay Nature Reserve, Western Australia, Australia, 34°55'S, 118°09'E, 5 February 1991, S.A. Halse, A.W. Storey (WAM 95/773).

Diagnosis

Penemideopsis angovensensis differs from *P. phreatica* as follows: projections covering openings of leg IV

not greatly enlarged (Figure 8); capitular bay projecting far forward of ventral shield (Figure 8); outer coxal margins not protruding (Figure 8); and its smaller size (e.g. dorsal shield 344 μm in *P. angovensensis*, 395 μm in *P. phreatica*). It differs from *P. pusilla* by the posterior margin of coxa IV not extending past the anterior margin of the genital field (Figure 8). It differs from both *P. phreatica* and *P. pusilla* by the lateral displacement of the dorsoglandularia such that the dorsoglandularial setae are situated far mesal of the glandularia (Figure 7).

Description

Male

Dorsal and ventral shields present. Lateral eyes present; medial eye present, but quite small (Figure 7). Dorsal shield (Figure 7) entire and ovoid, widest medially; bearing 3 pairs of sub-equidistant dorsoglandularia; dorsoglandularia laterally displaced such that dorsoglandularial setae situated far mesal of glandularia; postocularia well anterior to anterior-most glandularia of dorsal shield. Ventral shield (Figure 8) entire; vg1 situated near posterior margin of coxa II; all coxal suture lines visible, those between I and II, II and III, and III and IV posterior-laterally directed, thus forming acute angles with mid-line; medial margin of coxa IV broad, not extending past anterior margin of genital field; posterior margin of coxa IV rounded; outer coxal margins not protruding; openings of leg IV covered by small ventral lobes; capitular bay extremely deep and basally V-shaped, extending far forward of ventral shield; excretory pore incorporated into ventral shield. Genital field (Figure 11) with 3 pairs of small acetabula situated within field. Capitulum and chelicera basically as for *P. phreatica* (Cook 1986: figure 1611). Pedipalp (Figure 9) not uncate; tibia with large ventral projection bearing greatly enlarged spatulate seta; all setae acuminate. Legs (Figure 10) not modified and without swimming setae; without serrate setae; claws with ventral clawlets.

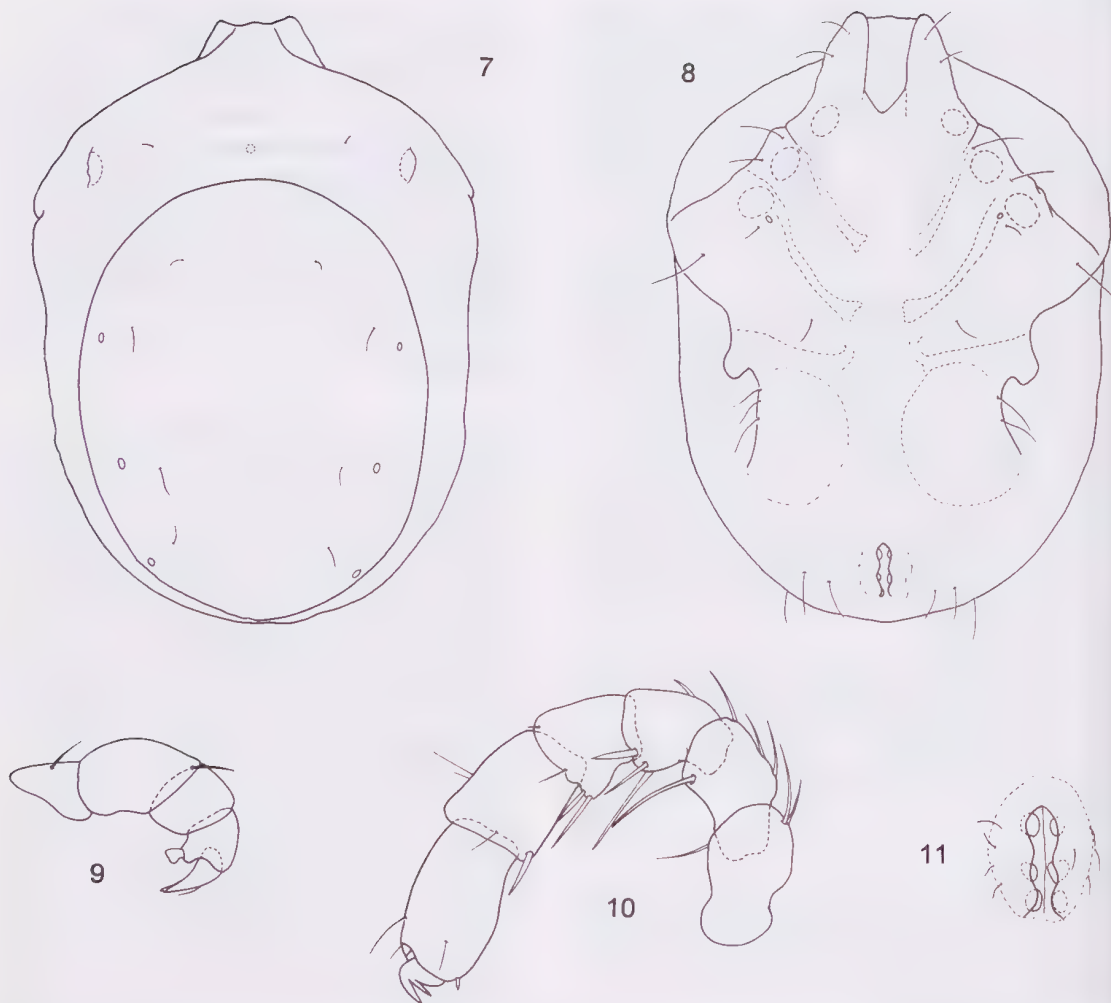
Dimensions (μm) ♂: dorsal shield 344/263, ventral shield 466/336. Pedipalp: trochanter 26, femur 49, patella 20, tibia 26, tarsus 26. Leg I: trochanter 54, femur 61, patella 38, tibia 39, metatarsus 52, tarsus 69. Leg IV: trochanter 78, femur 67, patella 52, tibia 61, metatarsus 78, tarsus 79.

Remarks

Storey *et al.* (1993) provide information regarding the type locality.

Etymology

The specific epithet refers to the type locality, Angove River.



Figures 7–11 *Penemideopsis angovensensis* sp. nov., holotype ♂: 7, dorsal shield; 8, ventral shield; 9, left pedipalp; 10, left leg I; 11, genital field.

ACKNOWLEDGEMENTS

I wish to cordially thank Dr Jenny Davis (Murdoch University) and Dr Stuart Halse (Department of Conservation and Land Management) for access to the fascinating specimens reported upon here.

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Manuscript received 12 October 1995; accepted 16 January 1996.

A new *Stygiochiropus* from a North West Cape (Western Australia) coastal plain cave (Diplopoda: Polydesmida: Paradoxosomatidae)

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Abstract – *Stygiochiropus peculiaris* sp. nov., is described from Camerons Cave, North West Cape, Western Australia. The new species is profoundly modified for cave life and its gonopods are more complex than in other *Stygiochiropus* species.

INTRODUCTION

Humphreys and Shear (1993) described a new paradoxosomatid genus, *Stygiochiropus*, for three new species found in caves in the Cape Range, North West Cape, Western Australia. One of these species, *S. communis*, is found in numerous caves throughout the karst region, while the other two, *S. isolatus* and *S. sympatricus*, are known only from single caves in the northern part of the generic range.

Camerons Cave (designated C [Cape Range karst area]452), from whence comes the new species described below, is not located in the Cape Range, but on the eastern coastal plain, at an altitude of ca. 13 m within the Exmouth town site. On the map published by Humphreys and Shear (1993; Figure 1), it would be placed about 4 km east of C-222, the type and only locality for *S. isolatus*. About 13 km to the northwest is C-111, type and only locality for *S. sympatricus*. The nearest cave with *S. communis*, the most widespread species, is 11 km southwest.

The cave is shallow and extends through the water table. The nature of the limestone in which the cave has formed is not known but appears to have formed in the Mowbowra Conglomerate, which comprises ridges of strongly calcretized gravel conglomerate, derived from Pleistocene shingle beachface (bar) deposits (Wyrwoll *et al.* 1993). The depth of the underlying Tulki limestone, within which caves containing the typical Cape Range fauna are found, is unknown.

Biologically, the caves on the coastal plain differ from those in the mountains. While some locally endemic genera of troglobites are in common, the species differ. An undescribed species of *Hyella* (Pseudoscorpionida) and a second species of *Draculoides* (Schizomida), *D. bramstokeri* Harvey and Humphreys, occur in Camerons Cave, along with undescribed ctenid and hahniid spiders, and a phalangodid opilionid. *Draculoides bramstokeri*

also occurs on Barrow Island (Harvey and Humphreys 1995), some 160 km to the northeast, and several aquatic troglobites have a similar distribution (Humphreys 1993); Barrow Island would have been connected to the North West Cape peninsula about 10,000 years ago at a time of low sea level.

Because of the unique biological significance of Camerons Cave, the new milliped species is being described to make the name available for protection efforts. Camerons Cave is the only known humid cave on the eastern coastal plain and, save for *D. bramstokeri*, is the only known locality for the several species it contains.

Stygiochiropus peculiaris sp. nov., is widely divergent from its congeners in bearing two additional gonopod processes on the femorite, as described below. This makes it tempting to regard the species as the most plesiomorphic of the genus, since troglotic adaptation often leads to gonopod simplification, not elaboration (Shear 1972), and the closest relatives of the genus have more complex gonopods with additional processes. However, *S. peculiaris* is probably as highly adapted to troglotic life as any of the other species, with a loose-jointed, elongate body, thin, brittle cuticle, and attenuate legs and antennae. The presence of this species in a cave formed in Pleistocene deposits is intriguing. It seems likely that *S. peculiaris* is older than the cave in which it occurs, and as with other *Stygiochiropus*, lives mainly within microcaverns, emerging into caves accessible by humans only when conditions are propitious (Humphreys and Shear 1993).

The new species was first noted in 1993 when a dead, dried specimen was collected. Subsequently, in early 1993, the cave was irrigated and plant litter was added (as described in Humphreys 1991), with the result that the fresh specimens described below appeared.

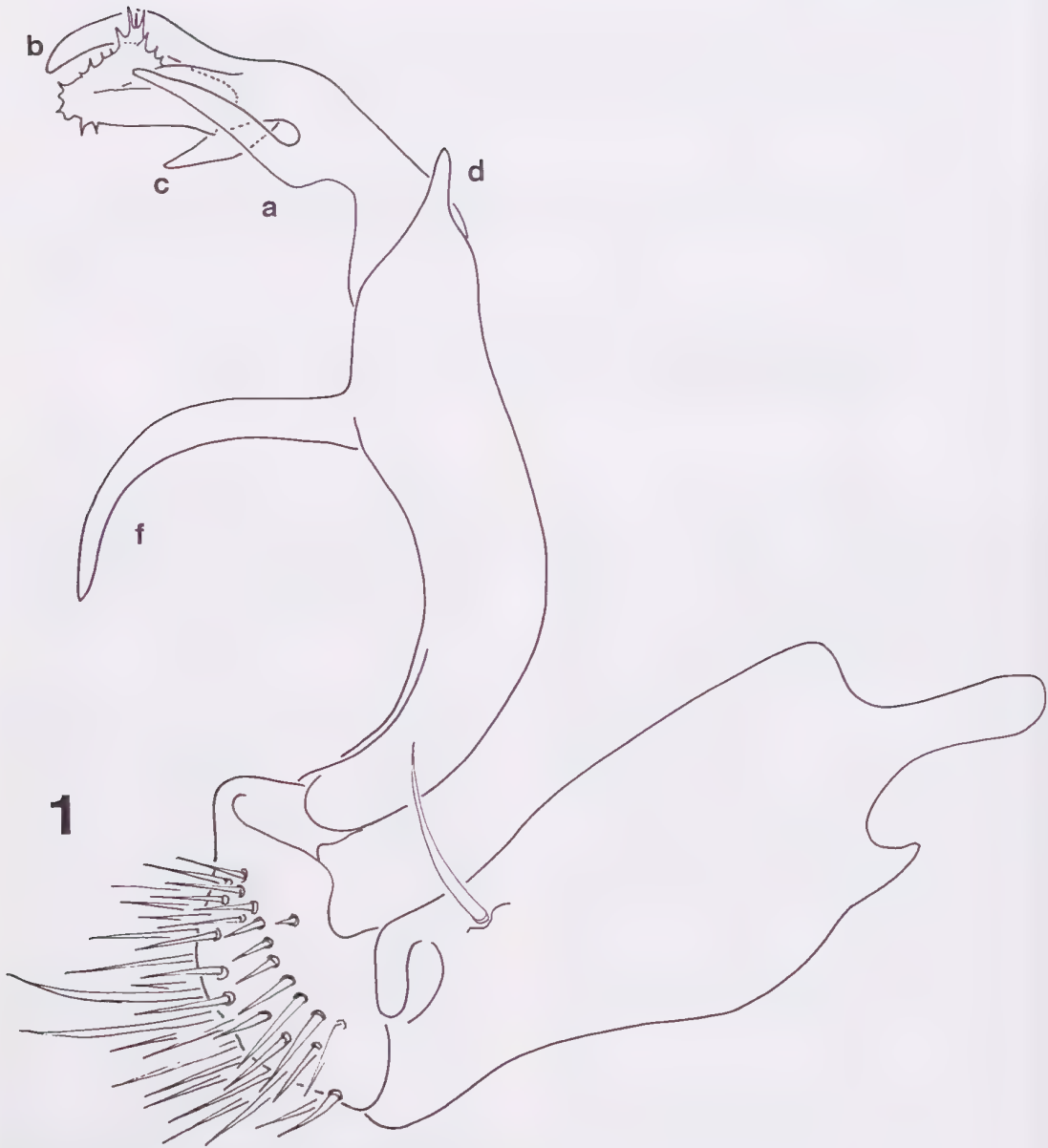


Figure 1 Left gonopod of *Stygirochirus peculiaris*, lateral view.

SYSTEMATICS

Family Paradoxosomatidae Daday

Subfamily Australiosomatinae Brölemann

Tribe Antichiropodini Brölemann

Stygirochirus Humphreys and Shear

Stygirochirus peculiaris sp. nov.

Holotype

♂, Cave C-452 (Camerons Cave), Exmouth town

site (21°57'56"S, 114°07'23"E), North West Cape, Western Australia, Australia, 11 January 1994, R.D. Brooks (WAM 95/480).

Paratypes

Fragments of juvenile, same collection data (WAM 95/481); dried and broken ♂, same locality, 10 August 1993, W.F. Humphreys, R.D. Brooks (WAM 95/482); 1 ♀, same locality, 28 August 1994, R.D. Brooks (WAM 95/483).

Diagnosis

Differing from all other species of the genus in the long process arising from the middle of the femorite.

Description

Male

Length, 13 mm; width at seventh metazonite, 1.0 mm; third antennal article 0.63 mm long. Nonsexual characters virtually identical to those described and illustrated for *Stygiochiropus communis* (Humphreys and Shear 1993).

Gonopods large and robust for size of animal, *in situ* with coxae and prefemora in contact, femorite then curves laterally and finally mesally so tips of gonopods touch in midline, femoral processes extending mesally and crossing. Prefemur short, less than 1/3 length of coxa, heavily setose, moderately curved. Prefemur/acropodite articulation well-formed, constricted. Femorite basally narrow, expanding to maximum width at base of median femorite process *f*; process long, thin, evenly curved, with acute tip. Distal femoral process *d* on lateral side subtending articulation of solenomerite. Solenomerite *s* broad, laminate, with marginal teeth. Process *a* as long as solenomerite, evenly tapering. Process *b* sickle-shaped, subequal to solenomerite. Process *c* short, acute.

Cuticle brittle, colourless.

Female

Length, 15 mm; width at seventh metazonite, 1.10 mm; nonsexual structures otherwise as in male.

ACKNOWLEDGEMENTS

The irrigation system was installed, maintained, and removed by Darren Brooks and the water provided courtesy of the Western Australian Water Authority. We thank R.L. Hoffman and D.G. Black for comments on the manuscript. The work was supported by grants from the National Estates Grants scheme to W.F. Humphreys.

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Manuscript received 3 July 1995; accepted 18 January 1996.

A new cavernicolous planthopper of the family Meenoplidae from New Caledonia (Hemiptera: Fulgoroidea)

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Abstract – A new troglobitic meenoplid species, *Eponisia hypogaea* sp. nov., is described from a limestone cave in New Caledonia, representing the first known cave-dwelling meenoplid species from the island. Notes on its ecology and generic placement are given.

INTRODUCTION

The Meenoplidae is one of the smaller families of planthoppers (Fulgoroidea) with only about 120 species. Epigean Meenoplidae are widely distributed in the Palaearctic, the Palaeotropics, Australia, and the western Pacific. The first cavernicolous meenoplid species, *Phaconeura pluto*, was described by Fennah (1973) from a cave in Nambung National Park, Western Australia. Subsequently, nine more cavernicolous Meenoplidae have been described from the Canary Islands (Remane and Hoch 1988; Hoch and Asche 1993), Western Samoa (Hoch and Asche 1988), Australia: Queensland (Hoch 1990) and Western Australia (Hoch 1993). Yet another cavernicolous meenoplid species is described here from Grottes d'Adio in New Caledonia and assigned to the genus *Eponisia* Matsumura. A synopsis of the world's cavernicolous Meenoplidae is given in Table 1.

The epigean meenoplid fauna of New Caledonia was studied by Fennah (1969) who found 8 species in 3 genera (*Eponisia*, *Nisia* Melichar and *Suva* Kirkaldy). Bourgoïn (pers. comm.) is currently reviewing the epigean Meenoplidae of New Caledonia, and will assess the generic placement of the new cavernicolous species in due course. The new species described here represents the second cavernicolous planthopper species from New Caledonia; the first was the troglobitic *Notuchus larvalis* Fennah (Delphacidae), described from Taphozous Cave, Hienghène (Fennah 1980).

The specimens are lodged in the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Queensland Museum, Brisbane (QM).

SYSTEMATICS

Family Meenoplidae

Genus *Eponisia* Matsumura

Eponisia hypogaea sp. nov.

Figures 1–8

Material Examined

Holotype

♂, Grottes d'Adio, New Caledonia, 21°15'S 165°15'E, dark zone, 21 February 1993, M.S. Harvey, N.I. Platnick, R.J. Raven (MNHN).

Paratypes

New Caledonia: 1 ♂, 1 ♀, same data as holotype (QM).

Diagnosis

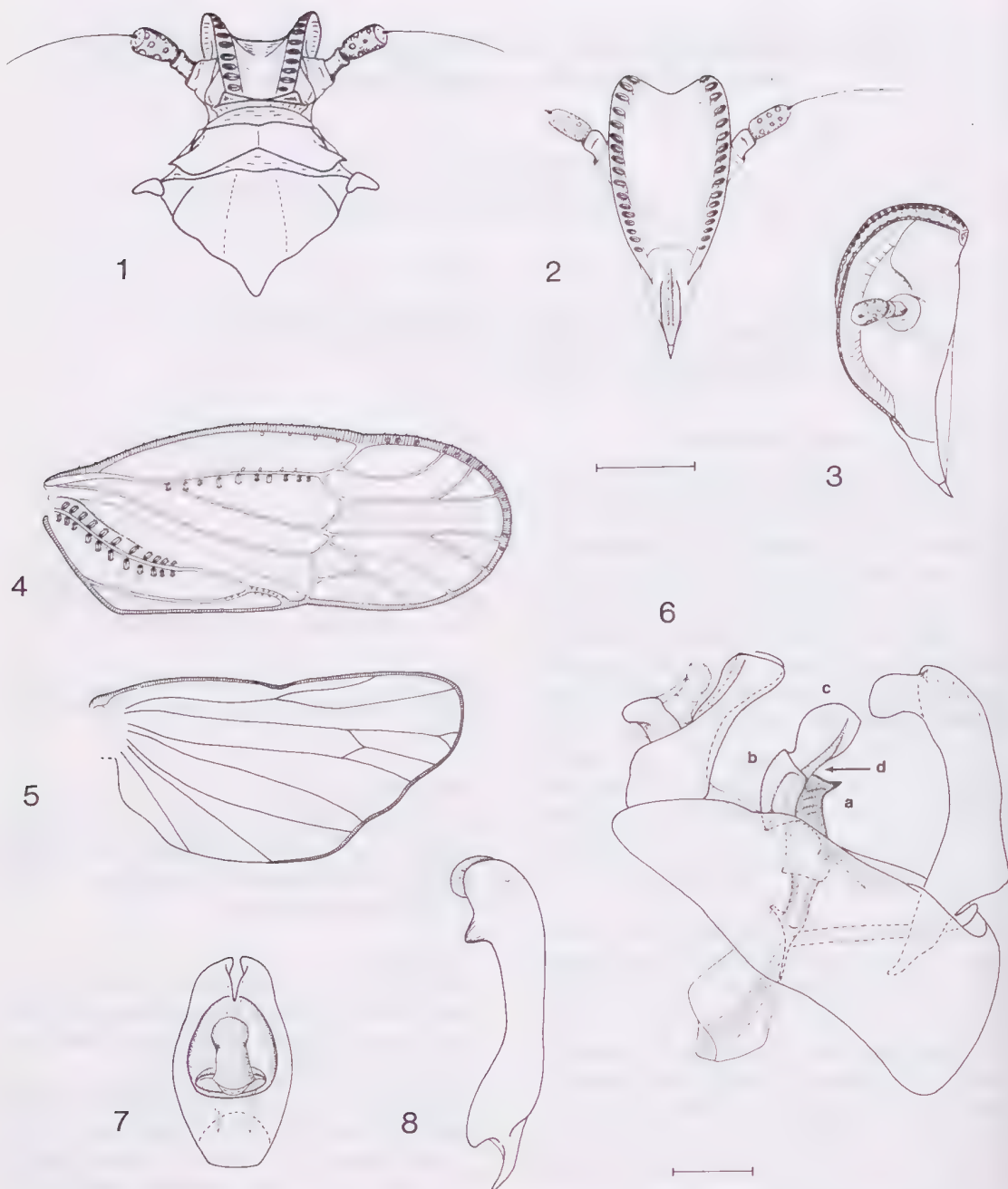
Cavernicolous. Small species with compound eyes, bodily pigmentation and tegmina reduced. Differing from other New Caledonian meenoplid species by these troglomorphic characters and by the male genital structures.

Description

Body length (equals distance between apex of head and tip of abdomen; measurements taken from specimens preserved in ethanol). Male: 3.2–3.8 mm (n=2). Female: 3.9 mm (n=1).

Body and legs pale yellow; tegmina shallowly tectiform, translucent, pale yellow, venation yellowish with areas of sensory pits white.

Head (Figures 1–3): vertex 1.6 times wider at base than long medially, continually rounded onto frons; posterolateral areolets small, triangular. Compound eyes and ocelli absent. Lateral margins of vertex and frons strongly ridged, directed anterolaterad, each bearing a row of oval sensory pits which ends at level of frontoclypeal suture. Vertex, frons and clypeus smooth, without median carina. Frons in frontal aspect with lateral margins slightly convex (maximum width of frons slightly below level of antennae), frons ca. 1.4 times longer medially than maximally wide, and ca. 1.6 times



Figures 1-8 *Eponisia hypogaea* sp. nov.: 1-3, holotype ♂; 4-8, paratype ♂: 1, head and thorax, dorsal aspect; 2, head, ventral aspect; 3, same, lateral aspect; 4, tegmen; 5, wing; 6-8, male genitalia: 6, pygofer, urite X, aedeagus, and gonostyles *in situ*, left lateral aspect; 7, urite X, dorsal aspect; 8, right gonostyle, ventral aspect. Scale line: 0.5 mm (Figures 1-5), 0.1 mm (Figures 6-8).

longer than post- and anteclypeus together. Lateral carinae of frons continuing onto postclypeus; frontoclypeal suture almost straight. First antennal segment short, second antennal segment

cylindrical, length ca. 1.4x width; indistinctly beset with sense organs.

Thorax (Figures 1, 4-5): pronotum smooth, with median carina obsolete. Pronotum medially about

0.6 times the length of vertex, and ca. 3 times as wide as vertex at base; posterior margin shallowly excavated. Mesonotum nearly planate, median carina absent, lateral carinae very faint. Tegmina reduced in length, 2.4 times longer than maximum width (= slightly proximad of clavus); in repose reaching anterior margin of genital segment; 8–9 apical cells; venation distad of nodal line individually variable; arrangements of sensory pits on tegmen as in other Kermesinae. Hind wings slightly reduced (anal field). Posttibia as in other Meenoplidae laterally devoid of spines, distally with six spines in a row. Postbasitarsus distally with five, second posttarsal segment with five spines in a single row. Postbasitarsus slightly longer than second and third posttarsal segments together. Pretarsal claws present, arolia well developed.

Male genitalia (Figures 6–8): pygofer in lateral aspect (Figure 6) ventrally ca. 5 times longer than dorsally, in caudal aspect figure-eight-shaped. Urite X (Figures 6, 7) in dorsal aspect longish ovate, distal portion medially deeply incised. Gonostyles (Figures 6, 8) moderately long, slender, subapically and medially with stout processes creating a claw-like impression. Aedeagus (Figure 6) in basal half ventrally with an unpaired, darkly pigmented, compressed, beak-shaped process (a) directed ventrad, dorsally with a rounded cap-like structure (b), triangular in dorsal aspect, extending laterad to margins of genital segment. Apical half of aedeagus consisting of a compressed, spatulate process (c) which is supported on each side by an integrated spine-shaped sclerite (d) (terminology of male genitalia *sensu* Bourgoïn and Huang 1990)

Female genitalia strongly reduced as in other Meenoplidae. Ventral valvifer distally angulate, ventral valvula globular, without any processes (terminology of female genitalia *sensu* Woodward 1957).

Distribution and Ecology

Eponisia hypogaea is known only from the Grottes d’Adio, New Caledonia. All specimens were collected “on tree roots well into the dark zone of the cave” (M.S. Harvey, pers. comm.). This observation and the well-developed troglomorphies (reduction of compound eyes, ocelli, bodily pigmentation, and, even if to a lesser extent, the tegmina) support the assumption that *E. hypogaea* is restricted to the deep cave zone (*sensu* Howarth 1981) and is therefore ecologically classified as troglobitic (obligate cavernicolous), although “they were able to hop or fly with remarkable speed and were difficult to catch” (M.S. Harvey, pers. comm.).

Remarks

Using Fennah’s key (Fennah 1969), the new cavernicolous meenoplid species would run to the genus *Eponisia* Matsumura which is based on the type species *E. guttula* Matsumura from Taiwan. However, according to Bourgoïn (pers. comm.), *Eponisia sensu* Fennah (1969) is polyphyletic, thus the cavernicolous meenoplid species cannot be placed into *Eponisia sensu strictu*, but should be placed in a separate genus, to be named by Dr Bourgoïn in due course. In the configuration of the male genitalia, the cavernicolous meenoplid species resembles the epigeal *E. matuta* Fennah from New Caledonia which is probably a close relative. On mere morphological evidence, however, it cannot be decided yet, whether or not *E. matuta* is even ancestral to *E. hypogaea*. Similar cases, i.e., the parapatric existence of apparently closely related epigeal and troglobitic species on the same island, as observed for example in Hawaii (Howarth 1980, 1981) have been fundamental to the development of a model to explain the evolution of terrestrial troglobites by adaptive shifts to novel habitats (adaptive shift model: Howarth 1980, 1986) rather than by adaptive events subsequent to the extinction of surface populations in the course of climatic changes (relict hypothesis: e.g. Barr 1968).

Table 1 Synopsis of cavernicolous Meenoplidae.

Canary Islands	<i>Meenoplus cancavus</i> Remane and Hoch, 1988 <i>Meenoplus charon</i> Hoch and Asche, 1993 <i>Meenoplus claustrophilus</i> Hoch and Asche, 1993
Western Samoa	<i>Suva oloimoa</i> Hoch and Asche, 1988
Western Australia	<i>Phaconeura pluto</i> Fennah, 1973 <i>Phaconeura proserpina</i> Hoch, 1993
Queensland	<i>Phaconeura minyamea</i> Hoch, 1990 <i>Phaconeura mopamea</i> Hoch, 1990 <i>Phaconeura crevicola</i> Hoch, 1990 <i>Phaconeura capricornia</i> Hoch, 1990
New Caledonia	<i>Eponisia hypogaea</i> sp. nov.

Etymology

The species name is derived from its subterranean habitat.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to Dr M.S. Harvey, Western Australian Museum, Perth, for the opportunity to study the meenoplid specimens, to Dr M. Asche, Research Associate, Bishop Museum, Honolulu, and to Dr Th. Bourgoïn, Muséum National d’Histoire Naturelle, Paris, for assistance and comments on the manuscript.

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Manuscript received 19 January 1994; accepted 19 January 1996.

Hesperopilio mainae, a new genus and species of harvestman from Western Australia (Opiliones: Caddidae: Acropsopilioninae)

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Abstract – *Hesperopilio mainae*, new genus and species, is described from Western Australia, based on specimens of both sexes. The new genus may be the most plesiomorphic of the subfamily.

INTRODUCTION

The opilionid genus *Acropsopilio* Silvestri (1904) was based on a Chilean species, *A. chilensis* Silvestri, and the genus was later used as a foundation for the family Acropsopilionidae by Roewer (1923). Soon, other acropsopilionine genera had been described: *Caddella* Hirst 1925, *Oonopsopilio* Lawrence 1931, *Zeopsopilio* Forster 1948, *Austropsopilio* Forster 1955, and *Tasmanopilio* Hickman 1957. In my 1975 review of the group, I recognized the affinities of the acropsopilionids with the northern hemisphere caddids, and placed Acropsopilioninae as a subfamily of Caddidae Banks 1895. I proposed *Oonopsopilio* as a synonym of *Caddella*, *Zeopsopilio* of *Acropsopilio*, and *Tasmanopilio* of *Austropsopilio* (Shear 1975). This latter synonymy was not accepted by Cokendolpher and Maury (1990), who argued that the form of the eyemound differed. However, I maintain it because of the very strong resemblances of the palpi of the two "*Tasmanopilio*" species to those of other *Austropsopilio*. Since writing in 1975, I have seen specimens of *Tasmanopilio fuscus* Hickman, and am firm in upholding my earlier conclusions. The main point of difference regards the eyemound, which in mainland Australian and Chilean *Austropsopilio* bears eyes which are not much enlarged and which extends on a short stalk out over the chelicerae. In the Tasmanian species *A. fuscus* Hickman, the eyes are intermediate in size but the eyemound is extended forward, while in *A. megalops* Hickman, the eyemound is sessile and the eyes are almost proportionally as large as in *Acropsopilio*. I find this transformation series in the eyes and the close resemblance of the palpi convincing evidence for synonymy.

The family Caddidae has one of the most interesting relictual distributions known. The subfamily Caddinae is known from eastern North America and Japan (Suzuki 1976); it consists of two living species, *Caddo agilis* Banks and *C. pepperella* Shear, and an Oligocene Baltic amber fossil, *C. dentipalpis* Koch and Berendt. I thought that the

smaller species, *C. pepperella*, originated as a neotenic isolate of *C. agilis* as recently as 15,000 years ago in adaptation to a shortened life cycle under periglacial conditions (Shear 1975). It so closely resembles juvenile *C. agilis* that even the type collection of the latter species was mixed. Suzuki (1976), in reporting both *Caddo* species from Japan, surmised that this could not be so, since there would be no way to account for the movement of *C. pepperella* from New England to Japan in so short a time. However, I think it entirely feasible that the Japanese populations are a second independent neotenic event, probably due to the same selection pressures. If this is true, although specimens from either population are indistinguishable in morphology, the Japanese isolate should have a new name. As an additional complication, both *C. pepperella* and *C. agilis* appear to be parthenogenic, with only three males of *C. agilis* ever reported among hundreds of specimens from many localities (Pennsylvania: Gruber 1974; Hokkaido: Suzuki and Tsurusaki 1983). However, given the Baltic Amber fossil *C. dentipalpis*, which seems nearly identical to living *C. agilis*, the Japanese and North American populations are probably relicts of a once much wider distribution for this species.

Amongst the acropsopilionines, *Caddella* consists of four South African species and would appear to be the sister group of the other two genera, which are more closely related to each other. *Austropsopilio* contains six species described from Australia, and an indeterminate number of species from Chile (Cokendolpher and Maury 1990). *Acropsopilio* has six nominate species. Two occur in Chile, and specimens of the genus have also been collected in Argentina and Brazil (Cokendolpher and Maury 1990). The South American members of the genus need re-examination as there may be additional species. Single species of *Acropsopilio* occur in Mexico, northeastern North America, New Zealand, and Australia.

With *Acropsopilio* and *Austropsopilio* already

known from the eastern coastal regions of Australia (Shear 1974; Cantrell 1980), it only remained to find an acropsopilionine as a relict in Western Australia. The requisite specimens were collected at Torbay Head in 1987, and at additional localities in southern Western Australia in 1995.

SYSTEMATICS

Family Caddidae Banks

Subfamily Acropsopilioninae Roewer

Hesperopilio gen. nov.

Type species

Hesperopilio mainae sp. nov.

Etymology

From *hesperus*, the west, and *opilio*, a shepherd, used as a combining stem in this group of harvestmen. The gender is masculine.

Diagnosis

The peculiar features of the palpus separate this genus from all other acropsopilionines: the femur lacks ventral spined tubercles and the tibia and tarsus are much reduced. Specifically, the reduction of the tarsus to a small appendage of the tibia and (in females) the shortened, swollen, globular tibia with many glandular setae, are not duplicated anywhere in the family. *Austropsopilio* have somewhat reduced tarsi, but the tibiae retain setose lobes and are normally cylindrical; in *Acropsopilio*, the setose lobes of the tibia are usually absent, but

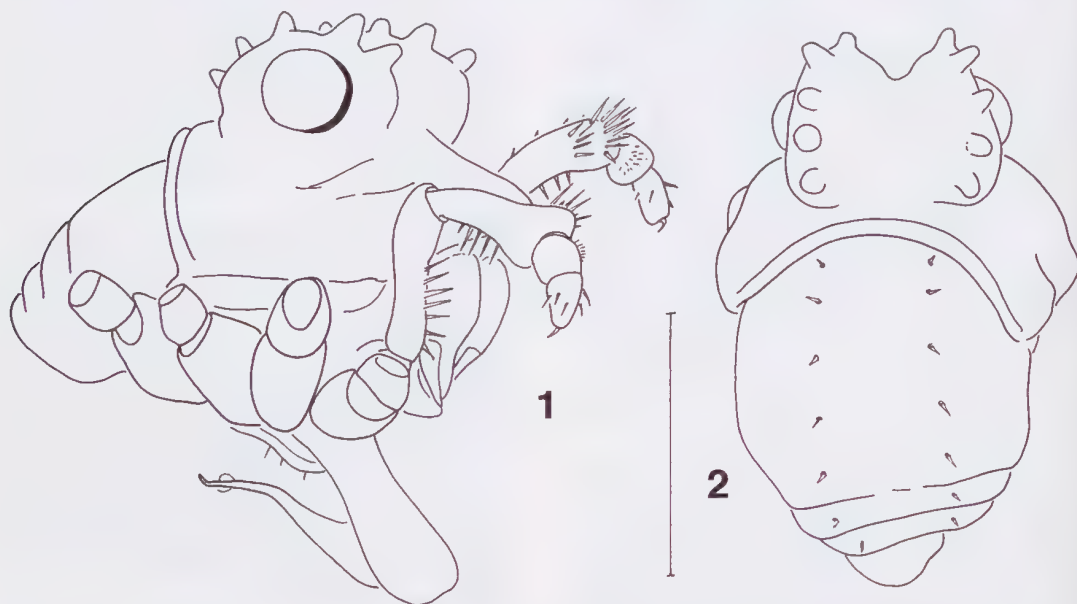
the tarsus is not reduced. *Caddella* species have essentially unmodified palpal tibiae and tarsi.

Males are known only in *Caddella* and *Austropsopilio*; the penes are complex, with accessory spines, and often exhibit torsion. The penis of *Hesperopilio mainae* is simple and acuminate, somewhat recalling the same organ in *Caddo agilis* (Gruber 1974). While some species of *Austropsopilio* have tuberculate bodies, none have the rows of tubercles above the eyes found in *Hesperopilio*.

Remarks

Cokendolpher and Maury (1990) claimed that *Austropsopilio* males were unknown until they found some in Queensland Museum collections (they excluded *A. fuscus*, males of which were described by Hickman [as *Tasmanopilio fuscus*, Hickman 1957]). They did not describe the specimens, but James Cokendolpher very kindly compared a drawing of the penis of *H. mainae* with his drawings of that of *Austropsopilio* species, and agreed that the Western Australian species represented a new genus. He pointed out that in *Caddella* and *Austropsopilio*, the other two genera with reduced palpal tibiae and tarsi, the penis is complex and spiny.

The palpi of *Hesperopilio mainae* converge to some degree on the palpi of the unrelated family Sabaconidae, in which a small tarsus reflexes against a swollen tibia, heavily set with glandular setae. Sabaconids collect prey by using the palpi as 'flypaper' and then rake them off the palpi with specialized cheliceral combs. While glandular



Figures 1, 2 *Hesperopilio mainae* n. gen., n. sp., ♂. 1, body, dorsal view; 2, same, lateral view. Scale line = 0.5 mm.

palpal setae are probably a basic character of opilionids, most acropsopilionines also have raptorial adaptations in the palpi. These seem minimized in *H. mainae*, while the glandular setae have become more important.

The relationships of *Hesperopilio* are difficult to assess. Because the penis resembles that of caddines (the immediate outgroup) and some phalangiids (the next outgroup), it is possible that this genus is the most plesiomorphic of the subfamily. On the other hand, male genitalia have not been described for *Acropsopilio*. Some or all of the species of this genus may be parthenogenic, but only *A. boopis* of eastern North America has been collected in quantity without the discovery of males. Based on palpal and available penial characters, it would appear that a reasonable arrangement for the subfamily would be (((*Hesperopilio* ((*Caddella* (*Austropsopilio*, *Acropsopilio*))).

***Hesperopilio mainae* sp. nov.**

Figures 1–9

Material Examined

Holotype

♂, Torbay Head (35°08'S, 117°38'E), Lot 40 (refers to a block of land, not a group of specimens), Western Australia, Australia, 20 April–14 May 1987, B. Y. Main (WAM 95/403).

Paratypes

Australia: Western Australia: 2 juveniles, same

collection data as holotype, but 5 October–2 November 1987 (WAM 95/404–5); 1 ♀, Stirling Range National Park, Bluff Knoll, 1070 m elevation (34°22'36.6"S, 118°15'10"E), 7 September 1995, S. Barrett (WAM 95/770); 1 ♂, same data as preceding ♀ but 900 m elevation (34°20'56.1"S, 118°14'54.7"E) (WAM 95/771); 1 ♂, Mt Lindsay, 410 m, (34°50'30"S, 117°18'21"E), 31 August 1995, S. Barrett (WAM 95/768).

Diagnosis

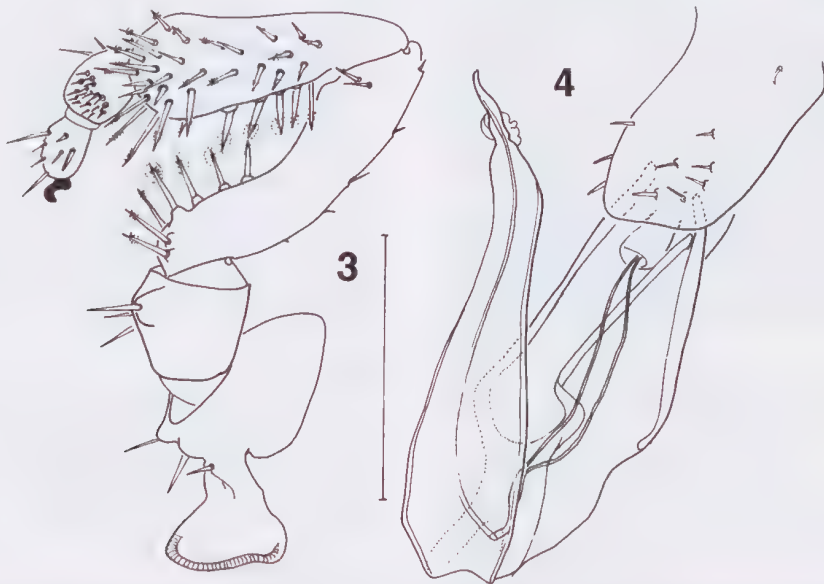
See the generic diagnosis.

Description

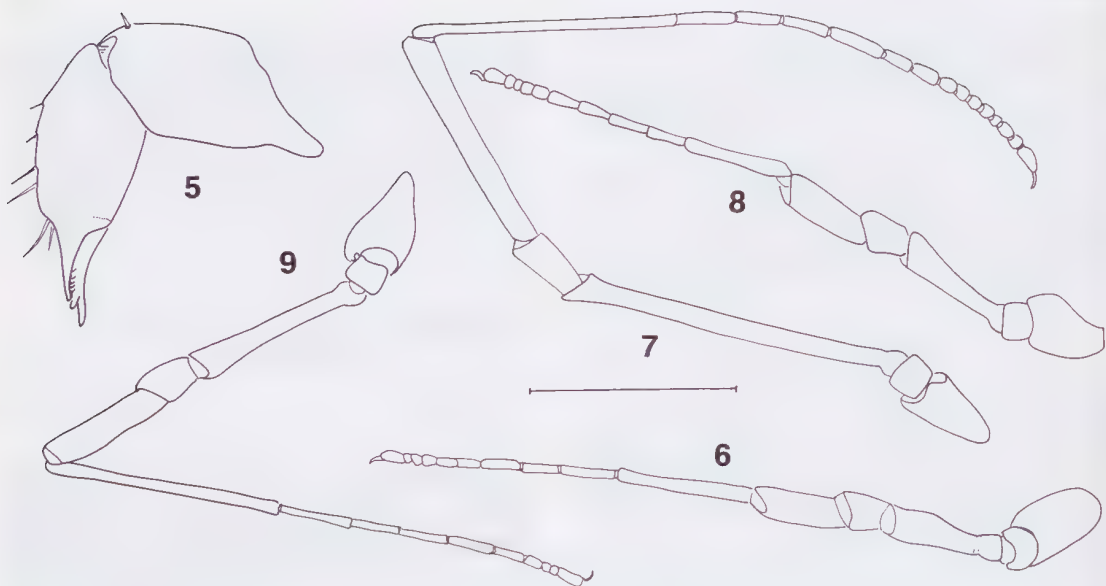
Male

1.25 mm long, 0.8 mm wide. Carapace about as broad as long, thoracic tergites not well marked, but with raised transverse ridge at posterior carapace margin; cuticle leathery, not heavily sclerotized. Eyemound nearly as wide as carapace (0.5 mm), strongly depressed between eyes, bearing series of five prominent tubercles over each eye. Eyemound not extending forward over chelicerae (Figures 1, 2). Ozopores not detected. Abdominal tergites not distinct, abdomen less voluminous than prosoma, soft. Abdominal sternites not distinct. Genital operculum (Figure 4) rounded, sparsely setose. Coxae and endites typical, similar to those of *Acropsopilio* species.

Chelicera (Figure 5) stout, largely unarmed, basal article 0.17 mm wide, 0.36 mm long, distal article 0.16 mm wide, 0.39 mm long. Fixed finger narrow, shorter than movable finger; movable finger 0.17



Figures 3, 4 *Hesperopilio mainae* n. gen., n. sp., ♂. 3, palpus, mesal view; 4, penis and genital operculum, ventral view. Scale line = 0.3 mm.



Figures 5–9 *Hesperopilio mainae* n. gen., n. sp., ♂. 5, chelicera, mesal view; 6, leg 1; 7, leg 2; 8, leg 3; 9, leg 4. Scale line = 0.3 mm for Figure 5, 0.40 mm for Figures 6–9.

mm long, with large subapical tooth, row of subequal smaller teeth on blade.

Palpus (Figure 3; lengths of articles given in Table 1) with trochanter robust, subquadrate, bearing three setae on ventral surface, mesal seta arising from prominent tubercle. Femur slightly sinuous, with row of six macrosetae on ventral surface of basal half; two small setae on mesal surface near distal end. Patella as long as femur, densely setose, drawn out mesoapically into large, globose lobe; ventrally with row of five macrosetae. Tibia reduced, subglobular, mesally with dense patch of about 20 small setae. Tarsus slightly longer than wide, subequal in length to tibia, with few dorsal setae, prominent curved claw lacking teeth.

Legs (Figures 6–9) in order of length 2:4:3:1; lengths of articles given in Table 1. Legs 1, 3 and 4 with 9 tarsal articles, leg 2 with 14.

Penis (Figure 4) with broad basal division strengthened ventrally with Y-shaped sclerotization, dorsally with single sclerotized bar, sharply bent posteriad at articulation with penis

shaft; shaft broad at base, narrowing to slightly less than half basal width. Glans sinuous, acute, tapering, with membranous inflated region at base.

Color light brown dorsally, darker on carapace around eyemound, with metallic highlights; paired white dots on each abdominal segment; palpi and chelicerae yellowish; legs dark brown, lighter distally.

Female

As described for male, but 1.6 mm long, 1.0 mm wide. Palpus (Figure 10) with trochanter bearing distinct ventral setose knob; femur with series of seven proximoventral setae, distomesal setose lobe at articulation with patella; patella lacking distal lobe, with five ventral setae, numerous setae on mesal surface; tibia subglobose, heavily setose; tarsus much reduced, with few setae and small claw. Ovipositor (Figure 11) with 12 darkly pigmented rings, distal nine with six setae each; labia with two series of six setae, distinct apical sense organs.

Distribution

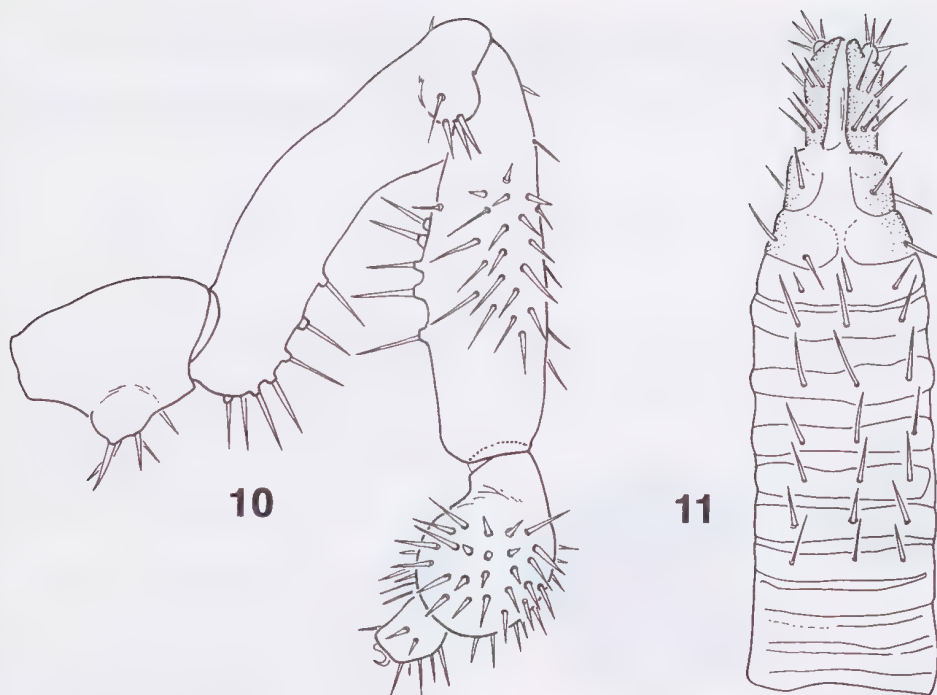
All specimens were taken in pitfall traps. The Mt Lindsay locality is about 40 km northwest of Torbay Head, while the Bluff Knoll sites are 100 km north-northeast. This indicates a fairly general distribution for the species in the area.

Etymology

It is my great pleasure to name this species for Barbara York Main, the collector of the holotype,

Table 1 Lengths of appendage articles of holotype *Hesperopilio mainae*

	TR	FEM	PAT	TIB	MTAR	TAR
palpus	0.15	0.34	0.34	0.11	–	0.08
leg 1	0.12	0.48	0.22	0.34	0.44	0.88
leg 2	0.14	1.40	0.26	0.86	1.02	1.56
leg 3	0.10	0.46	0.18	0.32	0.56	0.94
leg 4	0.12	0.72	0.22	0.46	0.94	1.26



Figures 10–11 *Hesperopilio mainae* n. gen., n. sp., ♀. 10, palpus, mesal view; 11, Ovipositor. Scale line = 0.3 mm.

who has for many years been a leading figure in Australian arachnology.

ACKNOWLEDGEMENTS

I thank Dr Mark Harvey, curator of arachnids at the Western Australian Museum, for sending the specimens to me, and James C. Cokendolpher and Glenn Hunt for their helpful advice.

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Manuscript received 3 July 1995; accepted 9 February 1996.

An unusual button-form australite from Earraheedy Station, Western Australia

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Australites collected from No.1 Marracoonda Paddock, which is centred 25°52'S, 121°53'E on Earraheedy Station, include an unusual form of button (Figure 1A–D). Flange has developed outward and unevenly instead of coiling backward from the direction of flight into a regular toroidal form. The dimensions of the button are 14.0–16.0 mm diameter x 7.1 mm thick and the weight is 1.51 grams.

The outwardly directed flange (Figure 1B) characterizes buttons of the unusual type studied by Chapman (1964), who reproduced similar shapes from glycerine glass in wind tunnel experiments and enunciated the aerodynamics.

Unlike the two buttons studied by Chapman, the Earraheedy button has no obvious flow ridges upon the anterior surface of flight (Figure 1D). However, the edge of the anterior surface has superimposed scallops (Figure 1C), and the low, eyebrow-like ridges bordering the scallops probably constituted a single, almost circumferential flow ridge of peculiarly scalloped shape.

The Earraheedy australite experienced a smaller ratio of body force to aerodynamic force (Chapman 1964) than the other known examples of its type, and has therefore a less exaggerated extension of the flange.

The type buttons and the one from Earraheedy Station are the only three on record but the form might not be as rare as would appear. Additional specimens could have been misidentified and dismissed as "button cores" i.e., buttons of the common type from which weakly attached flange had broken away. The deceptive similarity of the posterior surfaces of flight is illustrated by the Earraheedy button (Figure 1A) and a "button core" in the same collection from No.1 Marracoonda Paddock (Figure 1E). The anterior surface of the button (Figure 1D) shows that the irregular outline is a consequence of the different extents of the melt streams and not a consequence of fracture.

One of the type buttons was found within an area spanning the eastern half of the South Australia/Northern Territory border; the other was found near Gladstone, Tasmania. Those find sites and No.1 Marracoonda Paddock are within the two sectors of occurrence of very heavy

australites (Cleverly and Scrymgour 1978), but as there are only three known specimens, this distribution might be fortuitous.

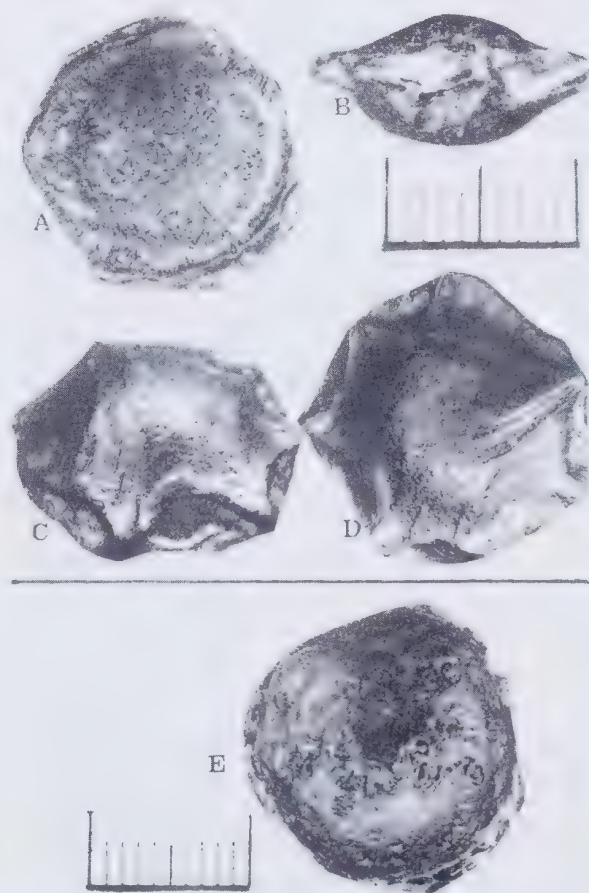


Figure 1 Two australites from Earraheedy Station. Scales are a centimetre divided into millimetres. A–D: Unusual button form. A: Posterior surface of flight showing deceptively broken-looking outline. B: Side view with direction of flight towards bottom of page showing stubby, outwardly directed flange. C: Oblique view of anterior surface showing three of the peripheral scallops with marginal flow ridge. D: Anterior surface of flight showing tendency to petaled shape. E: "Button core", posterior surface with broken outline resulting from loss of flange.

ACKNOWLEDGEMENT

The late Mr M.K. Quartermaine kindly lent me the australites from his collection and also processed my photographs (Figure 1).

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Manuscript received 13 September 1995; accepted 2 February 1996.

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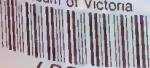
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Printed and published by the Western Australian Museum

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ISSN 0312 3162

Cover: Line drawing of *Sphenopteris* sp. A.
Illustration by Danielle Hendricks.

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Halacarines (Acari: Halacaridae) from Rottnest Island, Western Australia: the genera *Agauopsis* Viets and *Halacaropsis* gen. nov.

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Abstract – From Rottnest Island, Western Australia, four species of *Agauopsis* (*A. aequilivestita* sp. nov., *A. australiensis* sp. nov., *A. elaborata* sp. nov., and *A. ornatella* sp. nov.) are described. *A. aequilivestita* is most similar to the African *A. punctata* Bartsch. *A. australiensis* and *A. ornatella* are members of the wide-spread *microrhyncha* and *ornata* groups respectively. *A. elaborata* belongs to the *pugio* group, a natural group common in the southern hemisphere. The *Agauopsis hirsuta* group is raised to generic level with *Agaua hirsuta* Trouessart, 1889, as type species, and *Halacaropsis capuzina* gen. et sp. nov. is described.

INTRODUCTION

An inventory of the marine fauna in shores and shallows of Rottnest Island, Western Australia, resulted in the recovery of more than 80 halacarid species. The genera, and in parenthesis the number of species, found to date are: *Actacarus* Schulz (3), *Agaua* Lohmann (4), *Agauopsis* Viets (5), *Arhodeoporus* Newell (4), *Anomalohalacarus* Newell (1), *Australacarus* Bartsch (1), *Bradyagaue* Newell (1), *Copidognathus* Trouessart (ca 30), *Halacarellus* Viets (2), *Halacaropsis* gen. nov. (1), *Halacarus* Gosse (11), *Lohmannella* Trouessart (2), *Phacacarus* Bartsch (1), *Rhombognathus* Trouessart (10), *Scaptognathides* Monniot (1), *Scaptognathus* Trouessart (3), *Simognathus* Trouessart (7), and *Werthella* Lohmann (1). Studies in other areas of Western Australia and other substrata than studied around Rottnest Island are expected to raise the number of species and genera. In the present paper, four species of *Agauopsis* and one of *Halacaropsis* are described.

MATERIAL AND METHODS

In January 1991, the halacarid fauna of Rottnest Island, Western Australia, was surveyed. Various substrata, 10–500 cm³ each, were taken to the laboratory and the halacarids extracted by washing with a strong jet of water over a 100 µm sieve.

The mites were cleared in lactic acid and mounted in glycerine jelly. Drawings were prepared using a camera lucida. Holotypes and paratypes are deposited in the Western Australian Museum, Perth (WAM), other material in the Australian National Insect Collection, Canberra (ANIC), the Zoological Institute and Zoological Museum, Hamburg (ZIMH) and the author's halacarid collection.

Abbreviations used in the description and figures: a, alveolus; acp, accessory process; AD, anterior dorsal plate; ads, adanal setae (sixth pair of dorsal setae); AE, anterior epimeral plate; al, articular lamella; AP, anal plate; c, carina-like lamella; ca, canaliculi; cav, cavity; cp, central pit; dd, denticles; dl, dorsal lamella; ds, dorsal setae on idiosoma, ds-1, first pair of dorsal seta, ds-5, fifth pair of dorsal seta, ds-6, sixth pairs of setae (adanal setae); E, epimera; ep, epimeral pore; fa, lamella with famulus; GA, genitoanal plate; glp, gland pore; GO, genital opening; mcl, membrane of claw fossa; OC, ocular plate(s); ov, ovipositor; P, palp, P-2, second palpal segment; pa, porose areola; pas, parambulacral seta(e); pco, porose costa; PD, posterior dorsal plate; pds, pore from dorsal seta; PE, posterior epimeral plate; ri, ridge; sc, skeletal bars; so, solenidion; sp, spermatopositor; spl, spine-like lamella; spt, spermatheca; t, tines of pecten; vl, ventral lamella; vll, ventrolateral lamella. Legs numbered I to IV, leg segments 1 to 6, I-1, trochanter of leg I; II-2, basifemur of leg II; III-3, telofemur of leg III; IV-4, genu of leg IV; I-5, tibia of leg I; I-6, tarsus of leg I.

SYSTEMATICS

Genus *Agauopsis* Viets

Agauopsis Viets, 1927: 94.

Type species

Agaua brevipalpus Trouessart, 1889, by original designation.

Diagnosis

Idiosoma flattened, wide. Dorsum with AD, OC, PD and six, rarely five, pairs of idiosomatic setae;

sixth pairs of setae (adanal setae) in dorsal position. AE with three pairs of ventral setae and, generally, one pair of epimeral pores. Female typically with three pairs of pgs, male with 20–100 pgs close around the GO plus 0, one or two pairs of outlying setae. Gnathosomal base rectangular; rostrum parallel-sided. Basal pair of maxillary setae generally on base of gnathosoma, apical pair on rostrum. Palps four-segmented, attached laterally to base of gnathosoma. P-2 with one (rarely two) dorsal seta, P-3 with median spine or bristle. Leg I much wider than succeeding legs, bearing conspicuous spines. Tarsus I with three dorsal setae, dorsolateral solenidion, ventromedial spine, two unpaired ventral setae, and lateral and medial eupathid parambulacral setae. Tarsus II with solenidion dorsomedial in position. Paired claws on tarsus I smaller than those on succeeding tarsi. One larval and two nymphal stages.

Agauopsis aequilivestita sp. nov.

Figures 1–15

Holotype

♀, Duffield Ridge, off Rottnest Island, Western Australia, Australia, 30 m depth, medium to coarse sediment, 17 January 1991 (WAM 96/156).

Description

Female

Idiosoma 381 µm long, 230 µm wide. Most of dorsal plates with rather uniform porosity (Figure 1) which is made up by modified rosette pores. Each rosette pore typically with 6–9 canaliculi arranged along the borders of polygons; canaliculi running curved through the integument (Figure 2) and almost meeting in deeper layers. In centre of each polygon, surface of plate with very shallow central pit.

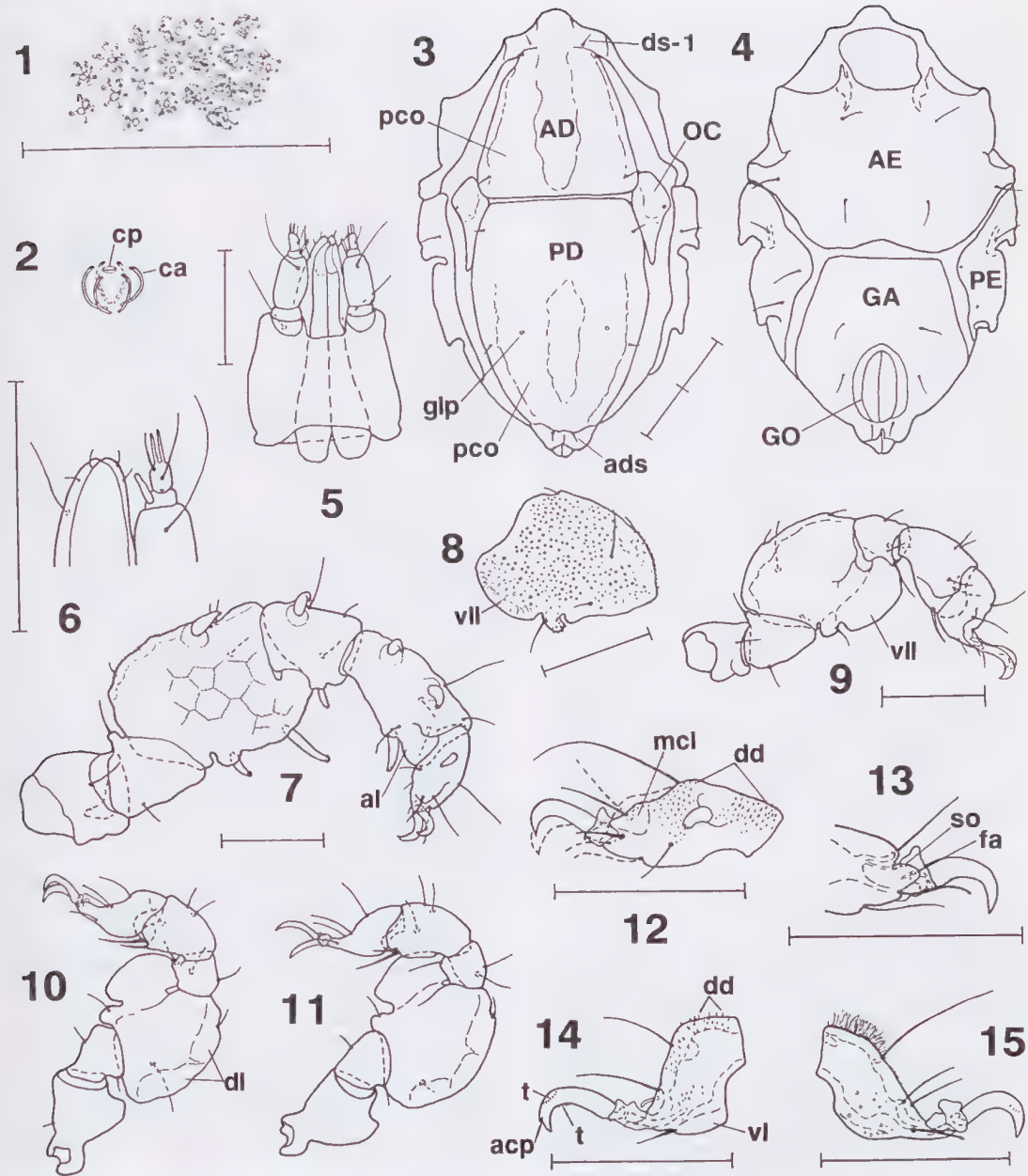
Anterior idiosoma (Figure 3) with rounded, dome-like frontal protuberance. AD anteriorly fused with dorsal portion of anterior epimeral plate; length of that plate, from posterior truncate margin to tip of frontal protuberance, 160 µm, width 130 µm. Two 25–40 µm wide porose costae joined posteriorly. Median area of plate with delicate pits, costae with canaliculi. Lateral portions of plate distinctly demarcated from abruptly raised porose area and densely studded with minute cuticular denticles. A pair of very delicate gland pores anterolateral to porose costae. OC 80 µm long, 32 µm wide, its posterior portion tapering. Corneae not seen. Anterior portion of OC with slightly raised porose areola, and with small gland pore and pore canaliculus in lateral margin. PD 202 µm long, 145 µm wide; its anterior margin truncate. Anterior portion and major parts of

raised wide median area of PD with very prominent porosity, a posterior oblong area without canaliculi. Lateral portion of PD beset with cuticular denticles. Pair of gland pores on level with insertion of leg IV. AD with setae ds-1 and ds-2, PD with setae ds-4, ds-5 and ds-6.

Marginal areas of ventral plates with small canaliculi, large ventral areas with delicate pycnic rosette pores; anterior AE and small transverse areas on GA with cuticular denticles. AE 132 µm long, 221 µm wide (Figure 4); posterior margin slightly concave. Epimeral processes I elongate; processes of epimera II lamellar. AE with three ventral setae. Epimeral pores not seen. PE with one dorsal and three ventral setae. GA 167 µm long, 145 µm wide. GO 65 µm long, 30 µm wide. Interval between anterior margin of GA and that of GO same as length of GO. Three pairs of pgs inserted as illustrated. Subgenital setae lacking.

Gnathosoma (Figure 5) 91 µm long, 66 µm wide. Gnathosomal base ventrally with small scattered pores, dorsally with delicate cuticular denticles. Rostrum and palps shorter than base of gnathosoma. Basal pair of maxillary setae on base of gnathosoma, the other pair inserted in apical third of rostrum. Chelicera 95 µm long. Dorsal seta on P-2 as long as length of that segment. Apical segments of right and left palp somewhat dissimilar in size, P-3 3 and 4 µm long and 6 µm wide, P-4 6 and 7 µm long and 4 µm wide. Medial 7 µm long spine of P-3 with truncate tip (Figure 6). P-4 with two setae and two apical spurs; length of two latter almost same as that of P-4.

Leg I (Figure 7) very wide; lateral flank of telofemur with conspicuous canaliculi, medial flank with reticulate pattern and delicate cuticular denticles. Genu, tibia and tarsus I laterally with cuticular denticles, dorsally with pits and medially again with denticles. Telofemur and tibia I each with large lateral articular lamella, I-3 also with about 6 µm high dorsal lamella. Telofemora II-IV very wide due to long, 20 µm high ventrolateral lamella, ventral protuberance and long, 11 µm high dorsal lamella; lateral flanks (Figure 8) with canaliculi, medial flanks with less conspicuous pores. Tibiae II-IV (Figures 9–11) with medial and lateral articular lamellae. Tarsus I shorter than tibia I; membranes of claw fossa (Figure 12) present though short. Tarsi II-IV each with ventral lamella, giving the tarsi a conspicuous truncate outline; dorsal and dorsolateral flank with cuticular denticles which often are tapering and filament-like. Membranes of claw fossae small. Leg chaetotaxy from trochanter to tarsus (solenidia excluded): leg I, 1, 2, 7, 5, 8, 8; leg II, 1, 2, 5, 4, 5, 5; leg III, 1, 2, 3, 3, 5, 4; leg IV, 0, 2, 3, 3, 5, 4. Leg I with wide, apically truncate and slightly dentate spines; telofemur with two ventral spines, 18 and 30 µm long, and one ventromedial spine; genu with



Figures 1–15 *Agauopsis aequilivestita* sp. nov., ♀: 1, portion of right PD anterior to gland pore; 2, diagram of modified rosette pore; 3, idiosoma, dorsal view; 4, idiosoma, ventral view; 5, gnathosoma, dorsal view; 6, tip of palp and rostrum, dorsal view; 7, leg I, medial view; 8, telofemur II, lateral view; 9, leg II, medial view; 10, leg III, medial view; 11, leg IV, medial view; 12, tarsus I, medial view (lateral setae and claw in broken line); 13, tip of tarsus I, lateral view (medial setae and claw omitted); 14, tarsus II, medial view (lateral setae and claw omitted); 15, tarsus IV, medial view (lateral claw omitted). Scale line = 50 µm.

12 µm long ventral spine and a distinctly longer ventromedial spine; tibia with 23 µm long ventral spine, and two ventromedial ones. Tibia II ventrally with spine-like, tapering bristle, ventromedially with short seta; tibiae III and IV

with pair of ventral tapering spines; ventrolateral spine larger than ventromedial one. Tarsus I (Figure 13) with 4 µm long solenidion obscured by 6 µm long membrane with canalicular famulus; pair of parambulacral setae singlets. Tarsus II

(Figure 14) with 5 µm long dorsomedial solenidium; apex with one slender ventral seta and a rather stout lateral pas. Tarsi III and IV (Figure 15) each with three dorsal setae and long medial pas. All tarsi with carpite-like sclerite.

Paired claws on tarsus I distinctly smaller than on succeeding tarsi. Neither accessory process nor pecten present. Paired claws on succeeding tarsi with accessory process and small pectines with delicate tines.

Male

Not seen.

Remarks

Agauopsis aequilivestita is closely related to *A. punctata* Bartsch, a species living on the eastern coast of northern Africa (Bartsch 1981). Differences are: length of AD relative to that of PD larger in *A. aequilivestita* than in *A. punctata*; setae ds-2 in *A. aequilivestita* inserted level with anterior OC, in *A. punctata* distinctly anterior to that level and removed from posterior angles of AD.

Agauopsis australiensis sp. nov.

Figures 16–38

Holotype

♀, Cape Vlamingh, Fish Hook Bay, Rottnest Island, Western Australia, Australia, *Amphiroa* sp. and other corallines, from beneath rock platform, just beneath low water edge, 15 January 1991 (WAM 96/157).

Paratypes

Australia: Western Australia: 1 ♂, data same as for holotype (WAM 96/158); 1 ♀, data as for holotype (ANIC); 1 ♂, 1 deutonymph, 1 protonymph, 1 larva, data as for holotype (WAM 96/159–162). 1 ♀, 1 ♂, data as for holotype (ZIMH A49/95).

Other Material Examined

Australia: Western Australia: 5 ♀, 2 ♂, 2 deutonymphs, 2 protonymphs, 1 larva, Fish Hook Bay, Cape Vlamingh, red algae *Liagora* sp. from beneath edge of rocky platform, 9 January 1991; 1 ♂, Nancy Cove, seagrass *Amphibolis* sp. with epiflora and fauna, 1 m depth, 12 January 1991; 2 ♂, Little Armstrong Bay, seagrass *Amphibolis* sp., 1 m depth, 16 January 1991; 1 ♀, Bickley Point, from epiflora and fauna on seagrass *Amphibolis* sp., 1–2 m depth, 18 January 1991. All in the author's collection.

Description

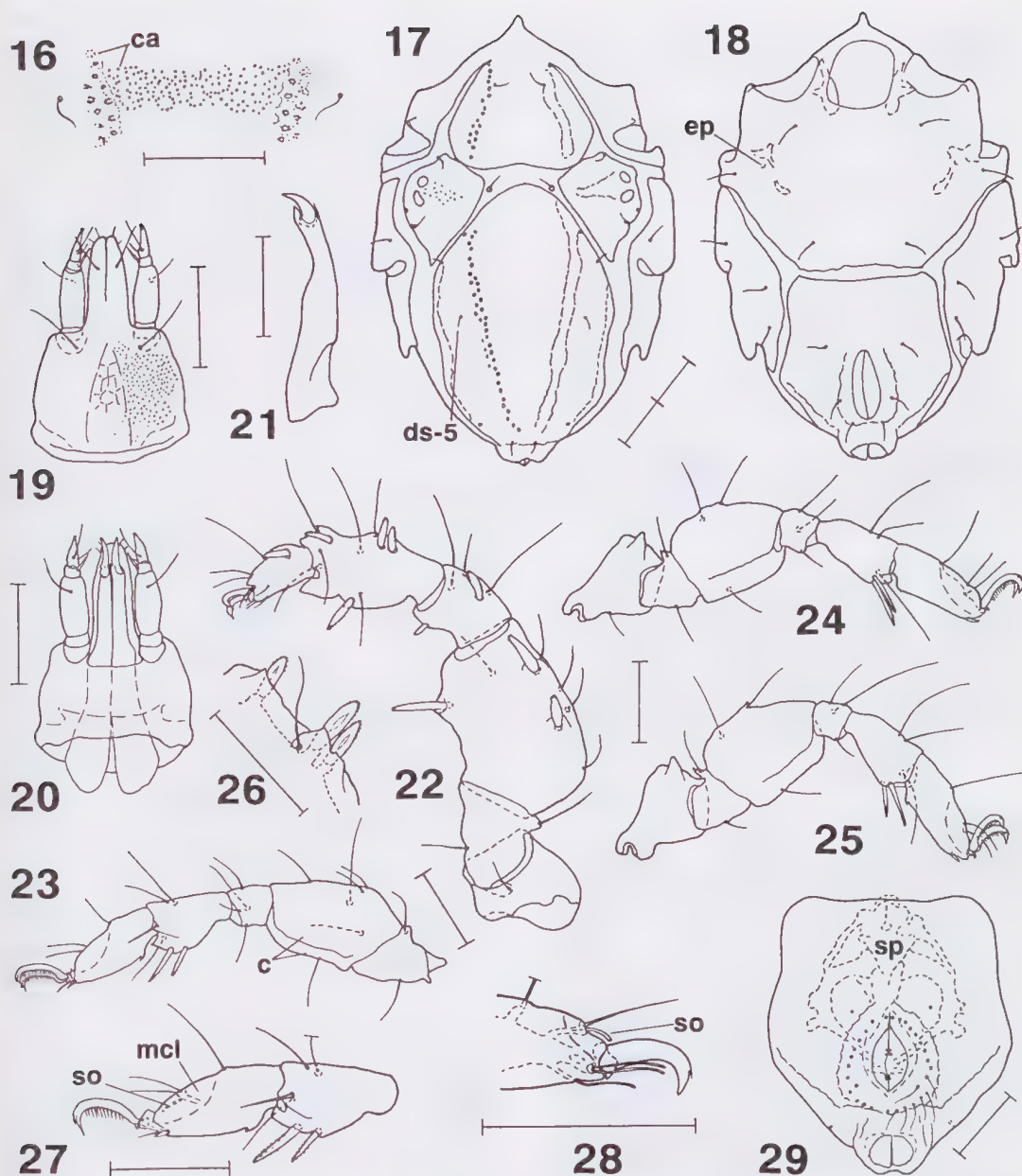
Female

Idiosoma 421–458 µm long, holotype 430 µm

long. Few coarse and parallel striae of membranous integument between large dorsal plates. Plates with raised, costa-like areas. Tegument of plates (Figure 16) traversed by canaliculi. Canaliculi within raised areas larger and arranged more densely than in remainder of plates; generally six to nine canaliculi assembled to groups (rosette pores); beneath each such group an alveolus present. Remainder of plate very faintly reticulated. AD fused with dorsal portion of anterior epimeral plate which in turn is prolonged into a bluntly ending frontal spine (Figure 17). The plate, from tip of frontal spine to posterior margin, 148 µm long, 139 µm wide. AD with pair of longitudinal costae, each two alveoli wide. Integument within transverse bar somewhat thicker. Pair of gland pores in lateral margin of AD immediately anterior to costae. OC 110 µm long, 73 µm wide. Two corneae near lateral margin. Medial to corneae triangular raised area with numerous groups of canaliculi present; alveoli lacking. Scattered canaliculi, a gland pore and a pore canaliculus present distolateral to posterior cornea. PD 248 µm long, 165 µm wide. Anterior margin rounded. Posterior portion of PD and anal plate fused. Pair of distinctly raised costae one to two alveoli wide. Lateral margin of plate somewhat thicker than remainder of plate but without alveoli. Pair of small gland pores in anterior PD, another pair in posterior PD. Dorsal setae ds-1 on AD, ds-2 in anterior edge of OC, ds-3 on small platelets within membranous integument between AD and PD, ds-4 in margin of PD level with insertion of legs III, ds-5 on PD lateral to costae, and ds-6 in posterior PD.

Ventral plates porose. AE 155 µm long, 278 µm wide. Pair of epimeral pores represented by small, 5 µm long slits at the surface and 5 µm wide sacculi in deeper integumental layers. Three pairs of setae as illustrated (Figure 18). PE with one dorsal and three ventral setae. GA 176 µm long, 161 µm wide. GO 65 µm long, 25 µm wide. Interval between anterior margin of GA and that of GO somewhat larger than length of GO. Proximal pair of pgs inserted slightly anterior level with anterior edge of GO. The other two pairs of setae near posterior portion of GO.

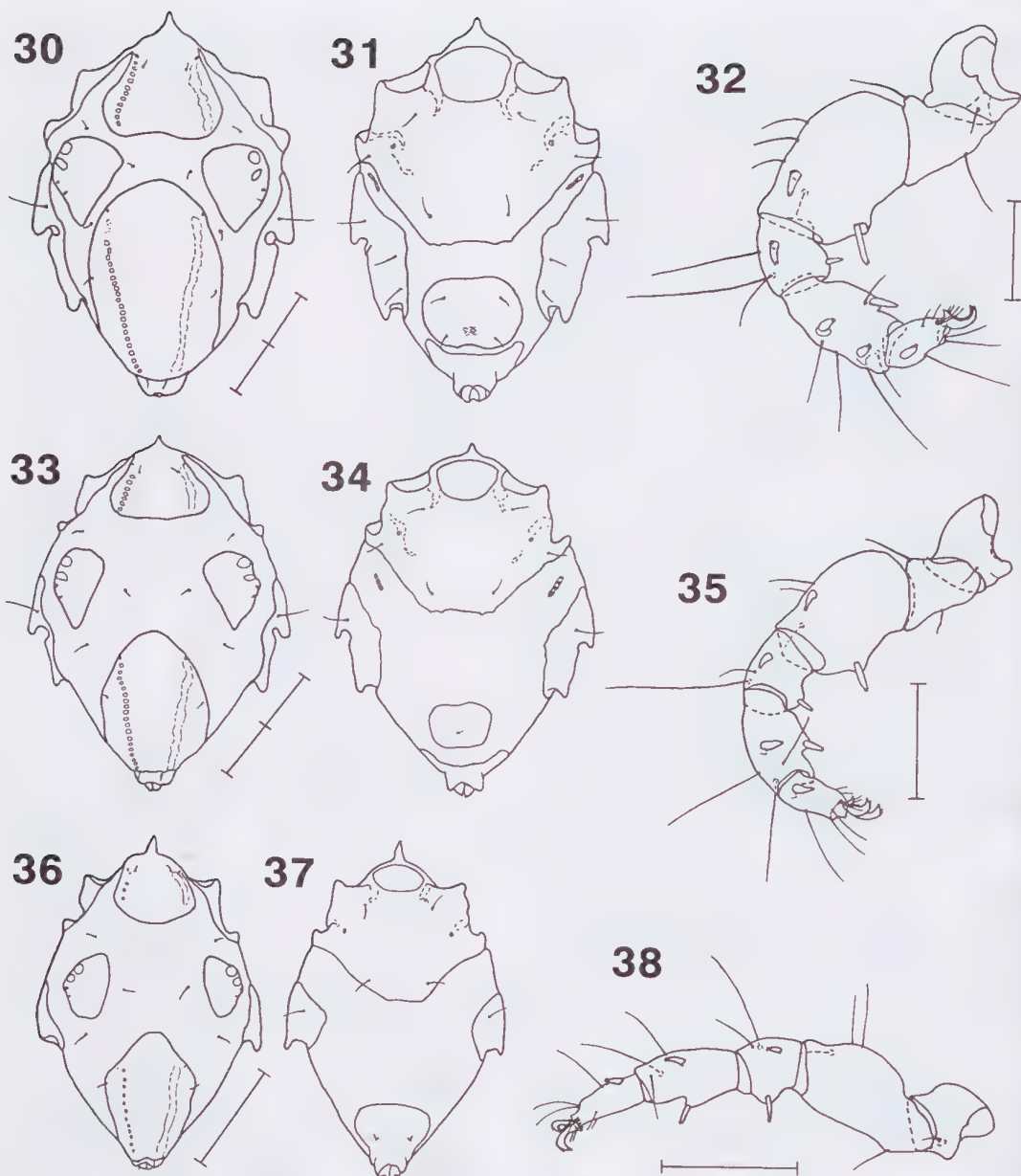
Gnathosoma 115 µm long, 78 µm wide. With coarse porosity in ventral and marginal portions of gnathosomal base and also within pharyngeal plate (Figure 19). Tectum truncate (Figure 20). Rostrum and palps shorter than gnathosomal base. Pair of long maxillary setae inserted on the base, another pair in distal third of rostrum; apex of rostrum with two pairs of rather long rostral setae. Median spine on P-3 longer than P-3. P-4 with two setae in basal whorl, one of which is shorter, the other longer than P-4. Chelicera slender (Figure 21), those of holotype 130 µm long, claw 21 µm long.



Figures 16–29 *Agauopsis australiensis* sp. nov.: 16, portion of PD between ds-5, ♀; 17, idiosoma, dorsal view, ♀ (left side shows alveoli from rosette pores, right side outline of raised areolae); 18, idiosoma, ventral view, ♀; 19, gnathosoma, ventral view, ♀; 20, gnathosoma, dorsal view, ♀; 21, chelicera, ♂; 22, leg I, medial view, ♀; 23, basifemur – tarsus II, medial view, ♀; 24, leg III, medial view, ♀; 25, leg IV, medial view, ♀; 26, ventromedial spines of tibia I, dorsal view, ♀; 27, tibia and tarsus II, medial view, ♀; 28, tip of tarsus I, lateral view, ♀ (medial setae and claw omitted); 29, genital plate, ♂. Scale line = 50 µm.

Trochanters III and IV with dorsal spine-like lamella. All telofemora (Figures 22 – 25) widened, lateral flanks with coarse porosity; medial flank of I-3 with very delicate porosity. Telofemora II to III each with 2-3 µm high ventrolateral and 7-9 µm

high ventromedial carina-like lamella and 3 µm high dorsal lamella. Ventrolateral articular lamella of I-5 large, ventromedial lamella very small. Lateral and medial articular lamellae of succeeding tibiae subequal in length. Tarsus I shorter than tibia



Figures 30–38 *Agauopsis australiensis* sp. nov.: 30, idiosoma, dorsal view, deutonymph (left side shows alveoli from rosette pores, right side outline of raised areolae); 31, idiosoma, ventral view, deutonymph; 32 leg I, medial view, deutonymph; 33, idiosoma, dorsal view, protonymph (left side shows alveoli from rosette pores, right side outline of raised areolae); 34 idiosoma, ventral view, protonymph; 35, leg I, medial view, protonymph; 36, idiosoma, dorsal view, larva (left side shows alveoli from rosette pores, right side outline of raised areolae); 37, idiosoma, ventral view, larva; 38, leg I, medial view, larva. Scale line = 50 μ m.

I. Tarsi on legs II–IV longer than tibiae; each with large lateral and medial membranes of claw fossa and small ventral carina with delicate spine-like process. Chaetotaxy of legs, from trochanter to tarsus (parambulacral setae included, solenidia

excluded): leg I, 1, 2, 8, 5, 10, 10; leg II, 1, 2, 6, 4, 6, 5; leg III, 1, 2, 3, 3, 5, 4; leg IV, 0, 2, 3, 3, 5, 4. Leg I with bluntly ending pectinate spines (Figure 26). Ventral spine on I–3 32 μ m long, two ventromedial ones 25 and 35 μ m long. Ventral spine on I–4 13 μ m

long, ventromedial one 25 μm . Ventral spine on I-5 25 μm long, ventromedial spines, from basal to distal, 20, 25 and 17 μm long respectively; the two basal spines inserted adjacent. Ventromedial spine on I-6 18 μm long. Spines on succeeding tibiae less stout. Tibia II (Figure 27) with two blunt, apically dentate ventromedial spines and a ventromedial bristle-like seta. Tibiae III and IV each with pair of slightly pectinate spines. Tarsus I with short membranes of claw fossa, dorsolateral membrane with 7 μm long solenidion (Figure 28); tip of tarsus with pair of doubled pas. Tarsus II with three dorsal setae, a spine-like ventromedial and a seta-like ventrolateral pas; solenidion, 8 μm long, placed on inner flank of medial membrane of claw fossa (Figure 27). Tarsi III and IV each with lateral spine-like pas; medially pore of seta but no seta present.

Paired claws of tarsus I with accessory process but no pecten. Bidentate median claw with small dorsal and rather stout ventral tooth. Paired claws on tarsi II-III with J-shaped pecten with about 20 medial tines on the flank and five minute lateral tines on the apex of the claw. Median claw present, its dorsal tooth absent, ventral tooth very small.

Male

Idiosoma 402–433 μm long, GA (Figure 29) of a 421 μm long paratype 180 μm long, 161 μm wide. GO 52 μm long, 34 μm wide, placed within 65 μm wide, raised area. Interval between anterior margin of GA and that of GO somewhat more than length of GO. A pair of outlying setae on level with anterior edge of GO and 30–31 pgs on raised area close around the GO. Spermatopositor almost twice the length of GO, 105–112 μm long, extending to 0.05–0.1 relative to length of GA (in Figure 29 spermatopositor somewhat dislodged). Genital sclerites with four pairs of small spur-like subgenital setae.

Deutonymph

Idiosoma 335–403 μm long. Plates somewhat smaller than those of adults. Setae ds-2 inserted in membranous integument anterior to OC (Figure 30), ds-5 in lateral margin of PD. Genital plate 62 μm long, 87 μm wide, not fused with anal plate (Figure 31). Genital plate with two pairs of pgs and two pairs of internal genital acetabula. Telofemur I with a ventral and a single ventromedial spine (Figure 32); tibia with a ventral and two ventromedial spines; setation of genu and tarsus I same as that of adults. Setation of tibiae II, III and IV same as known for adults.

Protonymph

Idiosoma 232–328 μm long (Figure 33). Dorsal plates smaller, their outline similar to those of deutonymph. Alveoli of porose costae

subrectangular. Genital plate 35 μm long, 50 μm wide, with a single pair of internal genital acetabula; pgs lacking (Figure 34). Telofemur, genu and tibia I each with one ventral and one ventromedial spine, tarsus with ventromedial spine (Figure 35). Tibia II with spine-like, delicately bipectinate ventral and short ventromedial seta. Setation of tibiae III and IV as in adults.

Larva

Idiosoma 232–248 μm long. Dorsal plates (Figure 36) more delicate than in nymphs. Porose costae of AD with three to four alveoli, costae of PD each with 12–14 rectangular alveoli. PD and anal plate contiguous. Anal plate (Figure 37) larger than in nymphs; plate with two spine-like protuberances. Except for median areas of AE and AP integument of ventral plates rather smooth. No spines on telofemur I (Figure 38); genu and tibia each with pair of spines; tarsus with ventromedial spine. Tibiae II and III each with pair of spine-like setae.

Variation

Several specimens have shorter ventromedial spines on leg I than has the holotype; in one male, e.g., the basalmost spine on I-3 is 19 μm long, the succeeding one 25 μm ; the ventromedial spine of I-4 is 20 μm long; the spines of I-5, from basal to distal, are 15, 20 and 15 μm , and the spine of I-6 15 μm long.

Remarks

Agauopsis australiensis is a member of the *microrhyncha* group. The most conspicuous character of this group is that tibia I has two of the three ventromedial spines inserted adjacent. Until now, 17 species have been described. In *A. australiensis*, as in the majority of species, the AD has a single frontal spine. *A. cryptorhyncha* (Trouessart), *A. felcis* Newell, *A. filirostris* MacQuitty, *A. insularis* Newell, and *A. paulensis* (Lohmann) are distinguished from these species by the tridentate or trilobed anterior AD. *A. antarctica* (Lohmann), *A. curvata* Krantz and *A. glacialis* Bartsch have a single spine which is bifid, rounded or rectangular, but not triangular. *A. mokari* Otto is unique in having four spines on telofemur I. *A. australiensis* is distinguished from the other species – *A. crassipes* (Gimbel), *A. humilis* Bartsch, *A. microrhyncha* (Trouessart), *A. pusilla* Viets, *A. racki* Newell, *A. robusta* Sokolov, *A. similis* Bartsch, *A. vineae* Newell – by its costae being narrow, one to two alveoli wide.

The species from southwestern Pacific, i.e. *A. similis*, from New Zealand (Bartsch 1979, 1985b), and *Agauopsis* sp., from Australia, Victoria, Philip Island – erroneously attributed to *A. similis* (Bartsch 1985b) – and *A. australiensis* can also be distinguished on the basis of insertion of ds-4

relative to anterior gland pore of PD. *A. australiensis* has a pair of gland pores distinctly anterior to the ds-4; in *A. similis*, the gland pores level with the ds-4, and in the species (a single female) from Philip Island, Victoria, the ds-4 insert anterior to the gland pores.

Agauopsis elaborata sp. nov.

Figures 39–49

Holotype

♀, Nancy Cove, Rottneest Island, Western Australia, Australia, corallines from rock platform, 20 January 1991 (WAM 96/163).

Description

Female

Idiosoma 310 µm long. Dorsal plates (Figure 39) with prominently raised porose areolae with modified rosette pores. Rosette pores with tube-like ostium, 4 µm deep, 2 µm in diameter; adjacent to ostia one to four canaliculi in deeper integumental layers. Remainder of plates with more or less distinct reticulate sculpturing.

Anterior margin of idiosoma rounded. An anterior dome-like area with 16 rosette pores; posterior pair of domes with about 30 pores each. AD fused with dorsal portion of anterior epimeral plate. Anterior plate, from anterior margin of idiosoma to posterior margin of the plate, 98 µm long, 87 µm wide. OC 95 µm long, 65 µm wide. Raised rounded areola, 25 µm in diameter, with about 20 rosette pores; dark-brown eye pigment beneath that areola. PD 170 µm long, 165 µm wide. From margins of deeply excavated median portion of the plate 25 µm long epicuticular filaments extending into the cavity (Figure 40). Pair of raised porose areolae swayed; widened on level with insertion of legs III, and dome-like on level with insertion of legs IV and in posterior PD. When focussing on deeper integumental parts, elaborate skeletal bars seen (Figure 40). Cavity beneath dome-like structures filled with epicuticular filaments. Pair of gland pores present in lateral margin of costae on level with insertion of leg III, another pair of pores in medial margin of costae on a level with insertion of leg IV. Setae ds-1 inserted within plate formed by dorsal fusion of anterior epimeral plate, ds-2 on OC at anterior margin of dome-like areola, ds-3 in anterolateral margin of PD. Setae ds-4, ds-5 and ds-6 enlarged, almost 50 µm long, directed towards the median cavity; ds-4 level with insertion of legs III, ds-5 level with legs IV, and ds-6 inserted posteriorly where PD and anal plate are fused.

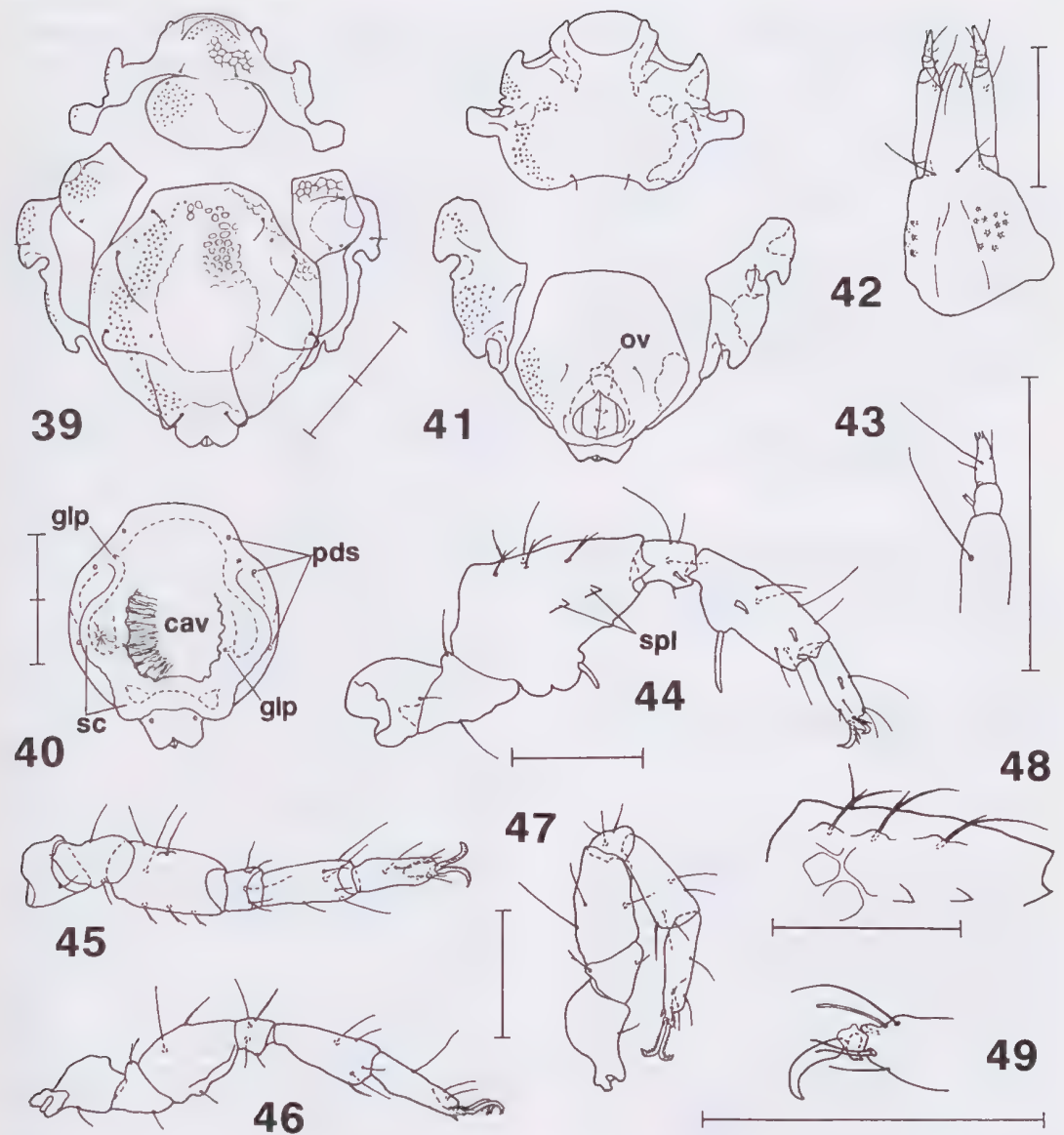
Ventral plates (Figures 41) with distinctly demarcated porose areolae, each pore represented

by small tube-like ostium which in deeper integumental layers is accompanied by two to four canaliculi. AE with three pairs of porose areolae, one marginal, one circular and one elongate crescentic one. PE with two marginal areolae and GA with pair of oblong areolae. Remainder of plate almost smooth. AE with very large cervical epimeral processes; coxal epimeral processes small, lamelliform. Insertion of trochanters II partly obscured by lamellar epimeral processes. AE 90 µm long, 197 µm wide, with three pairs of ventral setae; epimeral pores reduced. PE with one dorsal and three ventral setae. GA 140 µm long, 123 µm wide, with two pairs of pgs (a third pair thought to be present but obscured by protruding area with GO). GO 38 µm long, 35 µm wide. Interval between anterior margin of GA to that of GO equalling two times length of GO. Genital sclerites with two pairs of small subgenital setae. Ovipositor in rest extending beyond anterior margin of GO.

Gnathosoma 90 µm long. Base with pair of porose areolae, each areola with 10–11 modified rosette pores (Figure 42). Tectum truncate. Rostrum shorter than gnathosomal base, palps as long as base. Rostrum rather slender. P-3 5 µm long; its medial 2 µm long spine with serrate truncate apex (Figure 43). Medial seta on P-4 more than twice length of P-4.

Telofemur I (Figure 44) with two adjacent short and rounded basiventral lamellae, an almost 5 µm high dorsal lamella, two spine-like ventromedial lamellae and a pointed medial articular lamella. Lateral flank with reticulate sculpturing. Legs II–IV (Figures 45 – 47) slender; telofemora II–IV each with elongate but narrow ventrolateral lamella. Tibia II shorter than telofemur II; tibiae III and IV as long as telofemora respectively. Articular lamellae on tibiae II–IV lacking. Length of tarsi same or slightly less than that of tibiae. Tarsi II–IV with 12–15 µm long and 3–5 µm high membranes of claw fossae. Number of setae, from trochanter to tarsus: leg I, 1, 2, 6, 5, 9, 10; leg II, 1, 2, 6, 5, 6, 6; leg III 1, 2, 3, 4, 5, 5; leg IV, 1, 2, 3, 4, 5, 5. Ventral spine of telofemur I 13 µm long and placed on ventral lamella; ventromedial spines lacking. Ventral spine on tibia I 27 µm long, i.e. same as height of that segment; two ventromedial spines 6 and 5 µm long. Tarsus I with 5 µm long ventromedial spine. All spines with blunt, dentate tip. Succeeding legs lack spines. Dorsal setae on telofemora I (Figure 48) and II and basifemora III and IV clefted. Tarsus I with doubled pas; slender solenidion 10 µm long, inserted between dorsolateral seta and lamella with vestigial famulus (Figure 49). Tarsus II with three dorsal, one ventral seta and pair of single parambulacral setae. Tarsi III and IV each with three dorsal setae, a seta-like medial and a spine-like lateral pas.

Tarsus I with rather small paired claws which



Figures 39–49 *Agauopsis elaborata* sp. nov., ♀: 39, idiosoma, dorsal view (left side shows ostia from rosette pores, right side outline of raised areolae); 40, PD, showing internal skeletal bars, left side with filaments; 41, idiosoma, ventral view (right side shows ostia from rosette pores, left side outline of porose areolae); 42, gnathosoma, ventral view; 43, tip of palp, dorsolateral view; 44, leg I, medial view; 45, leg II, ventral view; 46, leg III, medial view; 47, leg IV, medial view; 48, dorsal portion of telofemur II, medial view; 49, tip of tarsus I, lateral view (medial setae and claw omitted). Scale line = 50 µm.

lack accessory process and pecten. Paired claws on tarsi II–IV with accessory process and pectines. Median claw reduced to small sclerite.

Male
Not seen.

Remarks

Agauopsis elaborata is a member of the *pugio* group – key group 6500 in Newell (1984) – a natural group characterized by its modified rosette pores with tube-like pores and small number of surrounding canaliculi; the dome-like porose

areolae; the ventral plates being rather smooth save of the demarcated areolae with modified rosette pores. Species belonging to this group are *A. chelipes* Bartsch, *A. delicatula* Newell, *A. estuarina* Newell, *A. mccaini* Newell, *A. papillata* Bartsch, and *A. pugio* (Trouessart). *A. delicatula* lacks the conspicuous porose areolae on AE characterizing the other species, but the chaetotaxy of the palps and legs agrees with that known of the *pugio* group.

A. elaborata is distinguished from all other *Agauopsis* on the basis of its PD with the internal, sinuose sclerites, its deeply excavated median portion filled with protruding epicuticular filaments, and its enlarged ds-4, ds-5 and ds-6.

Agauopsis ornatella sp. nov.

Figures 50–62

Holotype

♀, Cape Vlamingh, Rottneest Island, Western Australia, Australia, green algae from rock platform, upper tidal area, 15 January 1991 (WAM 96/164).

Paratypes

Australia: Western Australia: 2 ♀, same data as holotype (author's collection).

Description

Female

Idiosoma 297–310 µm long, 200–223 µm wide, holotype 310 µm long, 223 µm wide. Dorsal plates with distinctly raised areolae. Within these areolae (Figure 50) integument thicker than in surrounding plate, and deeper layers of integument bear subquadrangular alveoli, 2–3 µm long, 3–5 µm wide. Alveoli separated from each other by cuticular bars. Each alveolus with four to seven, rarely up to nine canaliculi piercing the integument and opening with small pores at the surface. Areas between raised costae with pits which are more or less distinctly arranged within polygons.

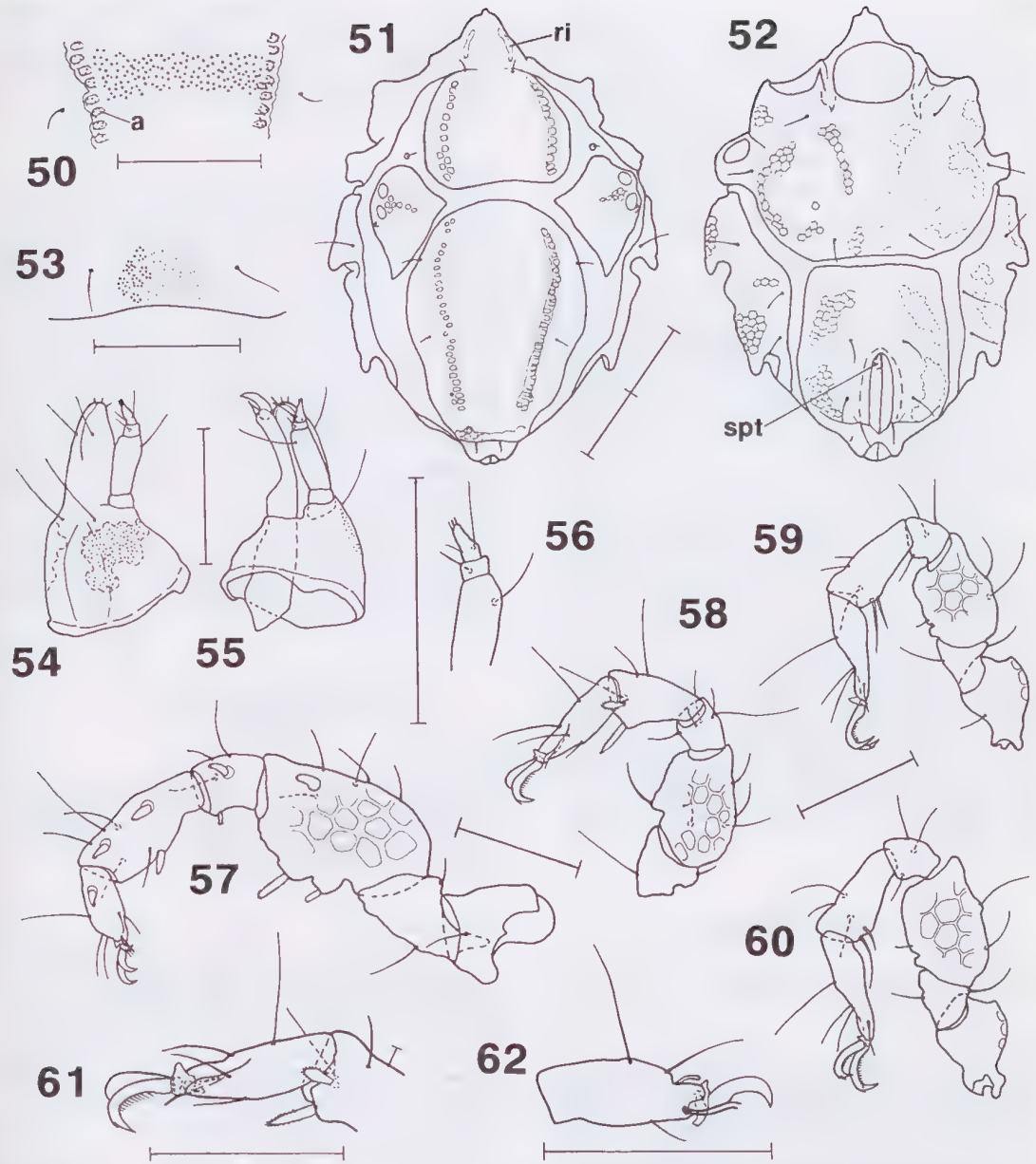
Dorsal portion of anterior epimeral plate (Figure 51) with 25 µm wide frontal process; that process with minute median spine and pair of approximately 20 µm long ridges. Length of anterior plate 115 µm (from tip of spine to the somewhat excavate posterior margin), width 97 µm. AD with pair of raised costae, major parts of these costae an alveolus wide, posterior portion of costae one to two alveoli wide. OC 78 µm long, 52 µm wide, with two distinct corneae and a transverse, raised porose areola. Gland pore and pore canaliculus almost adjacent in lateral margin of the plates. PD 165 µm long, 120 µm wide. Anterior margin rounded. Pair of longitudinal

costae not joined with transverse posterior bar. Anterior and middle portion of costae one alveolus wide, posterior portion two alveoli wide. Transverse bar two alveoli wide. Pair of gland pores present lateral to posterior portion of costae. Setae ds-1 inserted on level with insertions of leg I, setae ds-2 on 5 µm wide sclerite within striated integument between AD and OC, ds-3 not seen, ds-4 and ds-5 on PD level with insertions of legs III and IV, ds-6 posterior to transverse bar.

Ventral plates (Figure 52) with demarcated porose polygons, remainder of plates delicately pitted. Each porose polygon with 7–12 canaliculi (Figure 53). AE 100 µm long, 193 µm wide. Epimeral processes triangular, pointed. Area medial to insertions of legs II raised. Porose areolae garland-like, arranged as illustrated. GA 130 µm long, 98 µm wide, with two pairs of porose areolae. GO 55 µm long, 16 µm wide. Distance from anterior margin of GO to that of GA almost same as length of GO. Subgenital setae lacking. Anterior pair of perigenital setae level with anterior margin of GO. Ovipositor short, when at rest not reaching end of GO. Spermatheca 7 µm in diameter.

Gnathosoma 87 µm long. Gnathosomal base with pair of demarcated porose areolae (Figure 54). Tectum truncate (Figure 55). Rostrum 35 µm long. Palps extending somewhat beyond tip of rostrum. P-2 with long dorsal seta. P-3 4 µm long, its medial spine longer than P-3. P-4 10 µm long (apical spur-like setae included); with two basal setae, and apically with minute seta and two spurs (Figure 56).

Dorsal and medial flanks of telofemora (Figures 57–60) with wide reticulate sculpturing, lateral flanks with delicate reticulum. Telofemora II–IV with ventrolateral lamellae; articular lamellae lacking. Membranes of claw fossae reduced to small lamellae. Tibiae of legs I, II and IV shorter than telofemora of these legs, tibia III about as long as telofemur III. Tarsi of legs III and IV longer than tibiae. Leg chaetotaxy, from trochanter to tarsus (solenidion omitted): leg I, 1, 2, 8, 5, 8, 10; leg II, 1, 2, 5, 5, 5; leg III, 1, 2, 3, 3, 5, 4; leg IV, 0, 2, 3, 3, 5, 4. Two ventral spines on telofemur I 11 and 18 µm long, ventromedial spine 18 µm long; ventral spine on genu I 7 µm and ventromedial spine 15 µm long; ventral spine on tibia I 10 µm and the two ventromedial ones 16 and 11 µm long; ventromedial spine on tarsus I 10 µm long. Spines delicately pectinate. Tibia II (Figure 61) with a pectinate ventral and a short, wide and bipectinate ventromedial spine. Tibiae III and IV with pair of tapering bristles, the ventrolateral one distinctly longer than the ventromedial one. Tarsus I (Figure 62) with doubled pas; 5 µm long solenidion between dorsolateral seta and lamella with vestiges of famulus. Tarsus II (Figure 61) with three dorsal seta, a 6 µm long solenidion behind narrow medial



Figures 50–62 *Agauopsis ornatella* sp. nov., ♀: 50, portion of PD between setae ds-5; 51, idiosoma, dorsal view (left side shows alveoli from rosette pores, right side alveoli and outline of raised areolae); 52, idiosoma, ventral view (right side shows porose polygons, left side outline of porose areolae); 53, portion of AE between third pair of ventral setae; 54, gnathosoma, ventrolateral view; 55, gnathosoma, dorsolateral view; 56, tip of palp, lateral view; 57, leg I, medial view; 58, basifemur – tarsus II, medial view; 59, leg III, medial view; 60, leg IV, medial view; 61, tibia and tarsus II, medial view; 62, tarsus I, lateral view (medial setae and claw omitted). Scale line = 50 µm.

membrane of claw fossa, a ventral seta and a single lateral pas. Tarsi III and IV each with medial pas; lateral pas lacking. Solenidion on tarsus I 5 µm, on tarsus II 6 µm long.

Paired claws of tarsus I smooth, median claw

bidentate. Paired claws of tarsi II–IV with accessory process and pectines; the latter with about 10 tines.

Male

Not seen.

Remarks

Agauopsis ornatella is a member of the *ornata* group. The most prominent characters of this group are: porose areolae of dorsal plates with distinct alveoli and numerous canaliculi, ventral plates with garland-like arranged porose polygons. P-2 with tapering bristle-like spine. P-4 with two basal setae, an apical setula and two minute spurs. Legs with lamellae. Telofemur I with one ventromedial and two to three ventrolateral spines, tibia I with two ventromedial and one ventral spine. All tarsi with three dorsal setae. Tarsus II with lateral pas and ventral seta, and tarsi III and IV each with medial but no lateral pas. Members of the *ornata* group are *A. bacescui* Konnerth-Ionescu, *A. bermudensis* Bartsch and Iliffe, *A. inflata* Newell, *A. ornata* (Lohmann), and *A. pseudoornata* Bartsch. *A. punctata* and *A. aequilivestita* are very closely related with the *ornata* group but their ventral plates lack the garland-like porose areolae.

A. ornatella is characterized by its frontal process with the two narrow ridges, the costae on PD being a single alveolus wide, the rather narrow porose areolae on the AE and the area with the lateral garland being raised. The Philippine *A. pseudoornata* has a triangular frontal process with a pair of rounded porose areolae, the costae on the PD are three porose polygons wide, the porose areolae of the AE are distinctly wider (Bartsch 1985a). The eastern African *A. bacescui* has, compared with *A. ornatella*, a longer frontal spine, the costae on PD are two porose polygons wide, and telofemur I bears four spines (Konnerth-Ionescu 1977).

Genus *Halacaropsis* gen. nov.

Type species

Agaua hirsuta Trouessart, 1889.

Diagnosis

Dorsum with AD, OC and PD and the five pairs of setae ds-1 to ds-5. Adanal setae on anal plate, often in ventral position. AE with three pairs of ventral setae and pair of epimeral pores. PE with one dorsal and three ventral setae. Female GA with four to eight pairs of pgs and two to six pairs of subgenital setae. Male GA with about 50 perigenital setae close around GO; one or two pairs of setae may be outlying. Gnathosomal base quadrangular, rostrum parallel-sided. One pair of maxillary setae on gnathosomal base, one pair in distal rostrum. Palps four-segmented, attached laterally to base of gnathosoma. P-2 with dorsal seta, P-3 with dorsomedial seta, P-4 with three setae in basal whorl, one setula and two spurs apically. Leg I long and stout, telofemur, genu and tibia I with large spines; tarsus I with ventromedial

spine. Solenidion on tarsus I in dorsolateral position, on tarsus II in dorsomedial position. All tarsi with ventral setae. Median claw on all tarsi stouter than paired claws. One larval and two nymphal stages present.

Remarks

The genus *Halacaropsis* includes the species formerly assigned to the *Agauopsis hirsuta* group as defined in Bartsch (1986). *Halacaropsis* differs from representatives of the genus *Agauopsis* in the larger number of ventral setae on the tarsi I and II and the presence of ventral setae on tarsi III and IV. Moreover, tarsi of representatives of *Halacaropsis* have a remarkably enlarged median claw, much larger than that of *Agauopsis*; and the tarsi of the hind legs of *Halacaropsis* are rather slender, they may be somewhat curved. In juveniles of *Halacaropsis* are PD and anal plate widely separated, in juveniles of *Agauopsis*, PD and anal plate often are adjacent.

Halacaropsis resembles *Agauopsis* in the chaetotaxy of tibia I, and *Halacarus* in the number of ventral setae on the tarsi and the cerotegumental swellings on the plates.

Halacaropsis capuzina sp. nov.

Figures 63–87

Holotype

♂, Bickley Point, Rottnest Island, Western Australia, Australia, on seagrass *Amphibolis* sp. with dense epiflora and epifauna, 2 m depth, 18 January 1991 (WAM 96/165).

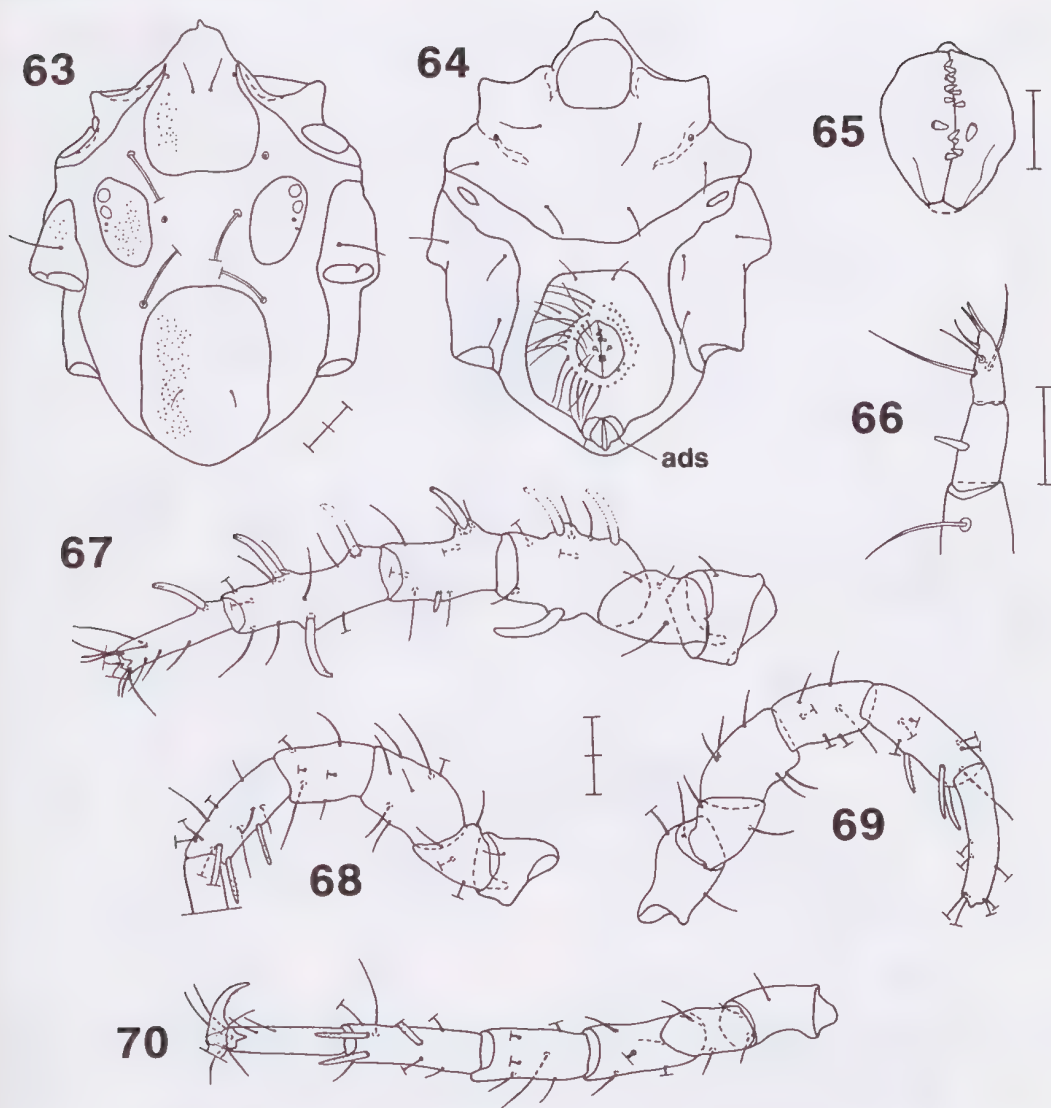
Paratypes

1 ♀ (WAM 96/166), data as holotype; 1 deutonymph, 1 protonymph, 1 larva (WAM 96/167–169), data as for holotype; 1 deutonymph, 1 protonymph (ANIC); 1 deutonymph, 1 protonymph, 1 larva (ZIMH A50/95), data as for holotype; 2 ♀, 3 deutonymphs, 5 protonymphs, 1 larva, data as for holotype (author's collection).

Description

Male

Idiosomal length 795 µm. All plates covered with delicate, almost smooth cerotegumental membrane, this membrane thickened in anteromedian portion of AD and posteromedian portion of PD. Integument of AD, OC, PD and dorsal portion of PE pierced by small pores (Figure 63). AD 272 µm long, 210 µm wide; anterior rounded margin with minute frontal spinelet. First pair of gland pores in lateral margin just anterior to level with insertion of leg I. OC 158 µm long, 100 µm wide, with two corneae, gland pore and pore canaliculus. Area



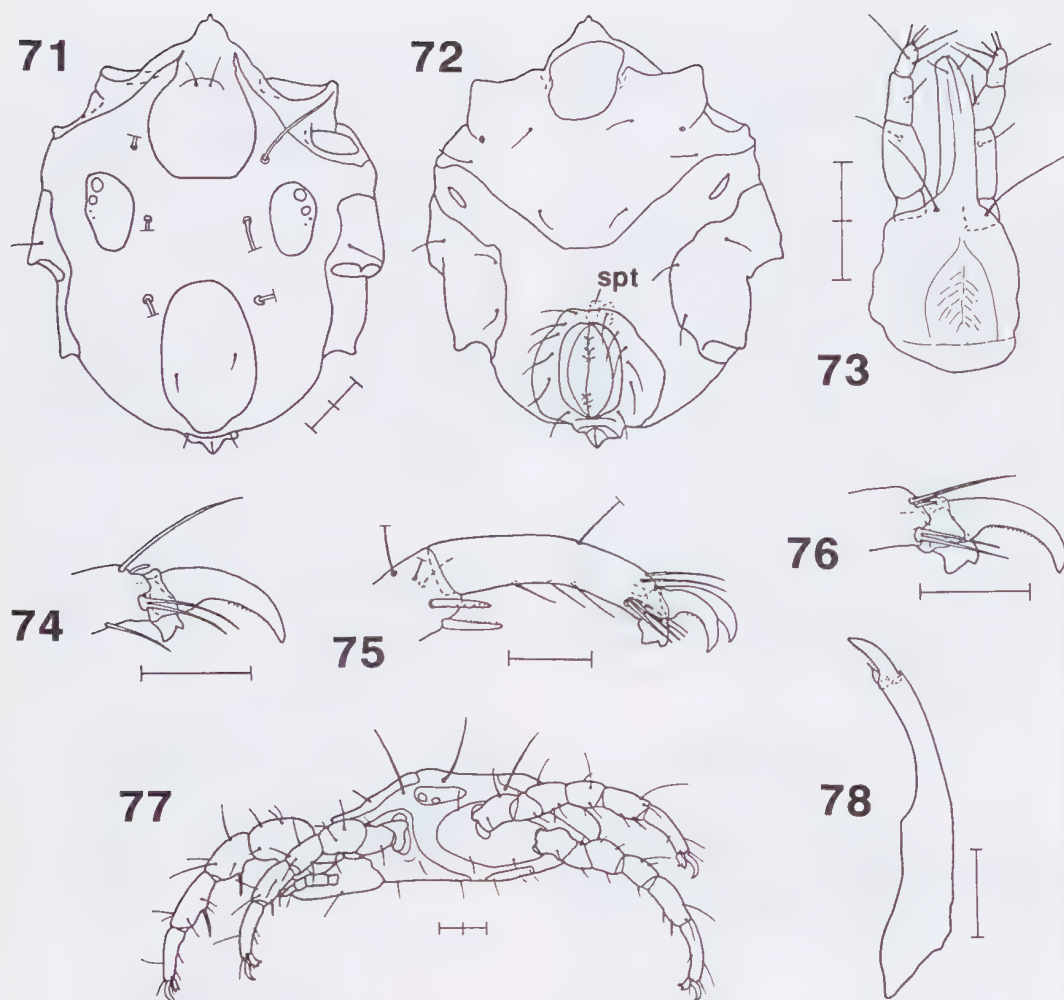
Figures 63–70 *Halacaropsis capuzina* sp. nov., ♂: 63, idiosoma, dorsal view (left side shows the minute pores); 64, idiosoma, ventral view; 65, genital sclerites; 66, tip of palp, dorsal view; 67, leg I, ventral view (broken spines completed with dotted lines); 68, leg II, medial view; 69, leg III, medial view; 70, leg IV, ventral view. Scale line = 50 μ m.

with corneae slightly raised. PD 322 μ m long, 230 μ m wide. Anterior margin broadly rounded, almost truncate. PD and anal plate separated by striated integument. Setae ds-1 inserted in middle of AD. Setae ds-2, ds-3 and ds-4 conspicuously strong, inserted on 20 μ m wide platelets within the striated integument. Small ds-5 on PD. Adanal setae on anal plate.

AE 242 μ m long, 557 μ m wide, with three pairs of ventral setae (Figure 64). Pair of epimeral pores adjacent to apodemes between EI and EII. PE with

a dorsal and three ventral setae. GA 322 μ m long, 255 μ m wide; its anterior margin truncate, angles rounded. GO 105 μ m long, 80 μ m wide. Interval between anterior margin of GO and GA almost same as length of GO. Fifty pgs close around GO, and one and a half pair of pgs outlying. Anterior pair of outlying setae close to anterior margin of GA. Genital sclerites each with seven blunt, spine-like subgenital setae (Figure 65).

Gnathosoma 260 μ m long, 128 μ m wide. Gnathosomal base rectangular; rostrum 130 μ m



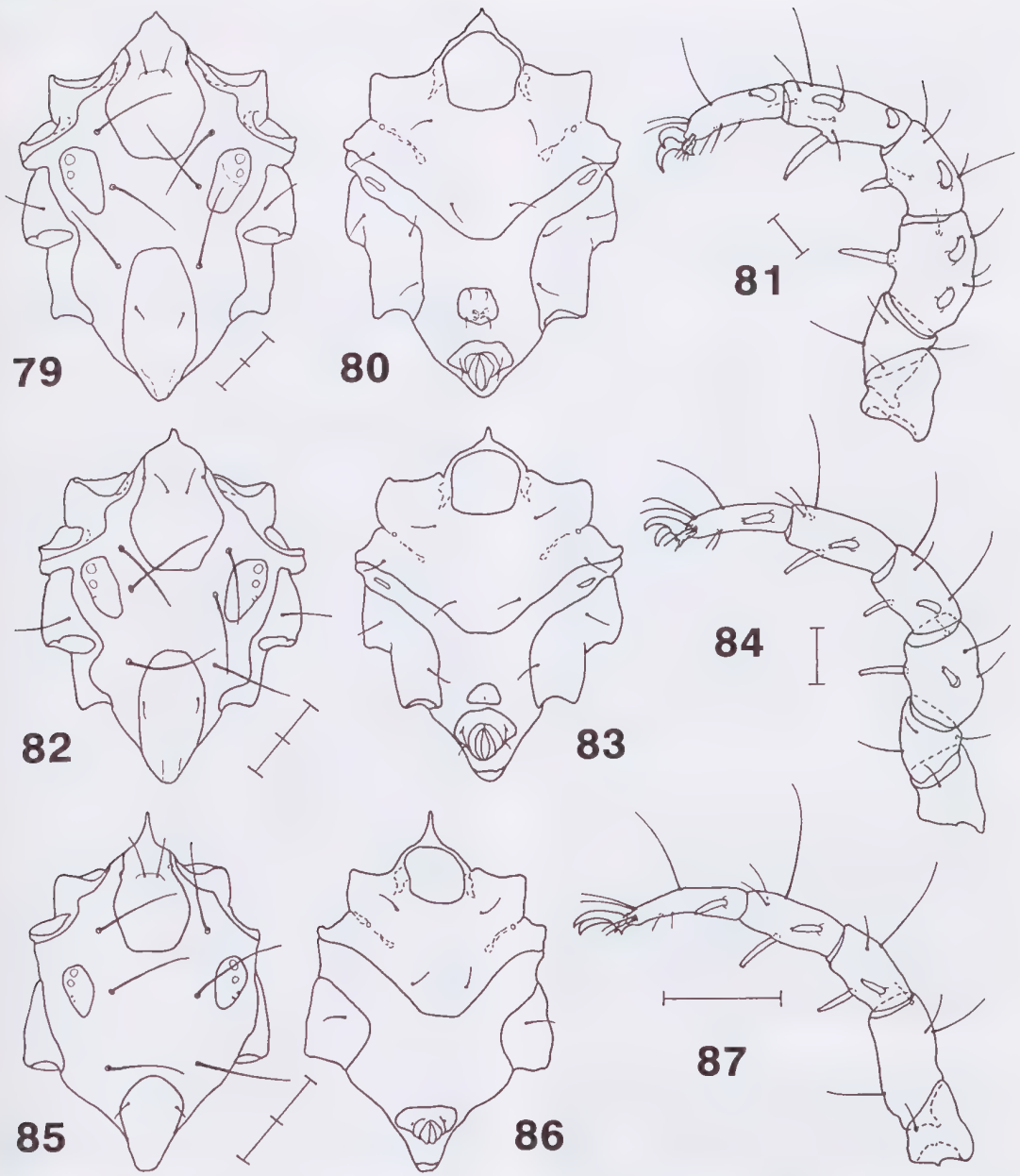
Figures 71–78 *Halacaropsis capuzina* sp. nov.: 71, idiosoma, dorsal view, ♀; 72, idiosoma, ventral view, ♀; 73, gnathosoma, ventral view, ♀; 74, tip of tarsus I, lateral view, ♀ (medial setae and claw omitted); 75, apex of tibia and tarsus II, medial view, ♀; 76, tip of tarsus II, medial view, ♀ (lateral setae and claw omitted); 77, deutonymph, lateral view; 78, chelicera, deutonymph. Scale line = 50 μm.

long, about as long as gnathosomal base. Basal pair of maxillary setae long; posterior pair of maxillary setae small, inserted close to tip of rostrum. Both pairs of rostral setae minute. Palps surpassing tip of rostrum. P-2 with dorsal seta; P-3 with dorsomedial blunt (broken?) seta (Figure 66). P-4 shorter than P-3, with three setae in basal whorl and apical setula and two spinelets. Elongate chelicera as figured for deutonymph.

Leg I (Figure 67) larger than the other legs (Figures 68–70) and longer than idiosoma; spines with blunt, delicately denticulate tip. Tarsus I shorter than tibia I; tarsi III and IV somewhat longer than tibiae III and IV respectively. Tarsi II–IV slightly bent. Numbers of setae from trochanter

to tarsus (solenidion omitted): leg I, 1, 3, 8, 9, 12, 12; leg II, 1, 4, 7, 6–7, 9–12, ?; leg III, 3, 2, 4–5, 5–6, 9–10, 7–8; leg IV, 3, 2, 5–6, 6–7, 9, 7. I-3 and I-5 both with one ventrolateral and two ventromedial spines; I-4 with pair of spines (left genu of holotype with both spines being stout, right genu with stout ventromedial and distinctly smaller ventrolateral spine). Tarsus I with three dorsal setae and a medial spine, one ventromedial and three ventrolateral setae, dorsolateral solenidion, and apical pair of doubled pas. Tibiae II–IV ventrally each with three delicately denticulate spines and one seta. Tarsi III and IV with two ventral setae and a pair of single pas.

All tarsi end with pair of slender claws and stout,



Figures 79–87 *Halacaropsis capuzina* sp. nov.: 79, idiosoma, dorsal view, deutonymph; 80, idiosoma, ventral view, deutonymph; 81, leg I, medial view, deutonymph; 82, idiosoma, dorsal view, protonymph; 83, idiosoma, ventral view, protonymph; 84, leg I, medial view, protonymph; 85, idiosoma, dorsal view, larva; 86, idiosoma, ventral view, larva; 87, leg I, medial view, larva. Scale line = 50 µm.

bidentate median claw. Paired claws with row of tines along ventral flank.

Female

Idiosomal length 670–750 µm. Anterior rounded AD with median spinelet (Figure 71), one specimen

without such a spine. AD of 670 µm paratype 242 µm long, 168 µm wide. OC 117 µm long, 68 µm wide. PD 235 µm long, 142 µm wide, more slender than PD of male, ds-5 inserted closer to margins of the plate than in male. AE 204 µm long, 483 µm wide, and GA 217 µm long, 207 µm wide. Anterior

margin of GA truncate; with six pairs of pgs (Figure 72). GO large, 142 µm long, 100 µm wide. Genital sclerites with five pairs of subgenital setae. Spermatheca 30 µm long, 35 µm wide. Gnathosoma as illustrated in Figure 73; dorsomedial seta on P-3 tapering and apically pointed. Tarsus I with 10 µm long solenidion between dorsolateral seta and lamella with canal from famulus (Figure 74). Tarsus II slightly longer than tibia II. Tarsus II (Figures 75, 76) with three ventral setae, 8 µm long solenidion adjacent to dorsomedial seta, and pair of doubled pas.

Deutonymph

Idiosoma (Figure 77) 524–603 µm long. OC and PD (Figure 79) smaller than plates of adults. Setae ds-5 near margin of PD. Quadrangular genital plate not fused with anal plate (Figure 80); its length 58 µm, width 62 µm; with two pairs of pgs, two pairs of subgenital setae and two pairs of internal genital acetabula. Anal plate in ventral position. Gnathosoma as in female with tapering pointed seta on P-3. Chelicera (Figure 78) elongate, its claw denticulate. Leg I (Figure 81) with number and arrangement of stout spines similar to that of adults. Tibiae II, III and IV each with two pairs of spine- or seta-like ventral setae. Tarsi I to IV with 3, 2, 1, 1 ventral setae respectively; tarsus I with doubled pas.

Protonymph

Idiosoma 410–503 µm long. Outline of dorsal plates (Figure 82) similar to that of deutonymph. Genital plate (Figure 83) 25 µm long and 35 µm wide; with single pair of internal acetabula; pgs and subgenital setae lacking. Telofemur, genu and tibia I each with pair of long spines (Figure 84). Tibiae II–IV each with a single pair of ventral setae. Tarsi I–IV with 2, 1, 0, 0 ventral setae. Tarsus I both medially and laterally with a large and a small pas.

Larva

Idiosoma 251–389 µm long. Frontal spine (Figure 85) much more slender than that of adults and nymphs. PD shorter than in nymphs. Genital plate lacking (Figure 86). No spines on femur I; genu and tibia I each with pair of spines; tarsus I with medial spine (Figure 87). Tibiae II and III each with pair of ventral setae. Tarsus II with one ventral seta; no ventral seta on tarsus III. Tarsus I, as well as the other tarsi, longer than tibiae of the legs. Tip of tarsus I medially and laterally each with a large and a small parambulacral seta.

Variations

In one of the adult specimens, the anterior idiosoma is evenly rounded, the others have a small frontal spinelet.

Table 1 Leg chaetotaxy of adult *Halacaropsis capuzina* (solenidia not included; spines in roman numerals)

segment	1	2	3	4	5	6
leg I	1	3	5–6+III	7+II	9+III	11+I
leg II	1	4	6–8	6–8	9–12	10
leg III	3	2	4–5	4–6	9–11	7–8
leg IV	3	2	4–6	6–7	9	7

The chaetotaxy of the legs varied and the number of setae of four adult specimens is summarized in Table 1.

Remarks

Halacaropsis capuzina is closely related to *H. warringa* (Otto), a species taken on the coast of New South Wales, southeastern Australia (Otto 1993). Both species are very similar in general facies, both have considerably enlarged ds-2, ds-3 and ds-4, the outline and chaetotaxy of the legs is almost identical. According to the material at hand, viz. four specimens of *H. capuzina* and six specimens of *H. warringa*, and the description by Otto (1993), the western and the southeastern Australian *Halacaropsis* can be discriminated on the basis of the anterior AD – wide rounded lobe terminating into a minute frontal spinelet (*H. capuzina*) vs trilobed, with two blunt lateral and a spine-like median lobe (*H. warringa*) – the ornamentation of the cerotegumental layer – smooth in *H. capuzina*, reticulate and with delicate filaments in *H. warringa* – and length of rostrum – as long (*H. capuzina*) vs shorter (*H. warringa*) than width of gnathosoma. The seta of P-3 is long, slender and evenly tapering at least in females and juveniles of *H. capuzina* (in old specimens it may be broken) but short and provided with a truncate spinose tip in both males and females of *H. warringa*.

The genus *Halacaropsis* includes the species *H. hirsuta* (Trouessart) **comb. nov.**, recorded from the Northern Atlantic and the Mediterranean (Viets 1940; André 1946; Chapman 1955), *H. warringa* (Otto) **comb. nov.**, taken on the coast of southeastern Australia, from coralline algae in areas exposed to moderate wave action (Otto 1993) and *H. capuzina*, abundant around Rottnest Island, with the adults living amongst the epifauna and flora on the seagrass *Anphibolis*, and the juveniles being more widely spread, present also within scrub-like corallines. The single *Halacaropsis*, a male, mentioned by Lohmann (1909) from Geraldton, Western Australia, differs from the specimens from southwestern and southeastern Australia in that its rostrum is much longer than the gnathosomal base, and the ds-3 are not enlarged but similar to the ds-1.

An undescribed species of the genus *Halacaropsis*,

distinctly differing from the Australian species, is recorded from South Africa (Bartsch 1986).

ECOLOGY

The two species *Agauopsis australiensis* and *Halacaropsis capuzina* were commonly taken in shallow water substrata, from intertidal to some few metres depth.

Juveniles of *Halacaropsis capuzina* were found in a wide range of habitats, regularly and in large numbers in samples with the seagrass *Amphibolis* as well as with coralline algae, whereas the adults were registered in seagrass washings. *H. capuzina* is thought to prefer the dense thicket of epifauna and flora on the seagrass. With the enlarged median claw and the slightly bent posterior tarsi, *H. capuzina* resembles representatives of the genus *Bradyagaue* which live on stolonaceous colonies. *H. warringa* and *H. hirsuta* are mostly recorded from samples with coralline algae (Chapman 1955; Otto 1993).

A remarkable feature of *H. capuzina*, as also of *H. warringa*, is the presence of long and very stout setae on the dorsum. These erect spines may both prevent its bearer from being swallowed by small fishes nibbling on the epifauna, and they may help to trap debris which serve as an optical and chemical camouflage.

Agauopsis elaborata, too, has conspicuously enlarged dorsal setae, but these setae are not erect but curved. Similar setae and an ornamentation resembling that of *A. elaborata* is described for *Thalassophthirius auster* Bartsch, *Copidognathus neptunus* Bartsch and *C. nasutus* Bartsch (Bartsch 1988, 1992a, 1994). The single specimen of *A. elaborata* and *C. nasutus* were found within corallines, *C. neptunus* was extracted from a dead coral block dredged in the Tolo Channel, Hong Kong; *T. auster* was taken from 13–34 m depth, Staten Island, South America, the substratum inhabited is not known.

A. australiensis, adults as well as nymphs and larvae, was taken from various substrata, from scrubs of corallines and calcareous tubes of polychaetes and together with *H. capuzina* from the epifauna and flora on *Amphibolis*.

In the collections gathered in January *Halacaropsis capuzina* was represented with rather large numbers of larvae, protonymphs and deutonymphs (only few of them were examined microscopically) whereas adults were sparse. In contrast to the juveniles, the four adult specimens available were intensely fouled with small algae and they lacked the claws on one or more legs. According to present knowledge, the majority of halacarines have a univoltine life cycle with either short or prolonged periods of reproduction (Bartsch 1989). *H. capuzina* obviously belongs to the

former category, with egg deposition within few weeks in early spring, larvae hatching in the spring, juveniles predominating in the summer months, and adults being present in autumn, winter and spring. The heavily fouled adults found in January obviously belong to the parental generation. *Agauopsis australiensis* has a less distinctive period of reproduction, adults are abundant also in summer months.

The larvae of both *H. capuzina* and *A. australiensis* have a slender, pointed frontal spine. These frontal spines may help the hatching larvae to rupture the egg membrane. The anterior spinelet of larvae of *Halacarellus psammophilus* (Krantz) and *H. subcrispus* Bartsch is thought to be such an egg bursting mechanism (Krantz 1976; Bartsch 1978).

BIOGEOGRAPHICAL REMARKS

According to present records, five representatives of *Agauopsis* and two of *Halacaropsis* live in Western Australian shallow waters, these are *A. aequilivestita*, *A. australiensis*, *A. elaborata*, *A. ornatella*, a representative of the *Agauopsis furcata* group (Bartsch 1993), *Halacaropsis capuzina* and *Halacaropsis* sp. (Lohmann 1909).

A. australiensis, *A. ornatella* and *A. elaborata* are members of the *microrhyncha*, *ornata* and *pugio* groups respectively. The *microrhyncha* group is wide-spread, present in warm as well as polar waters; most species are known from the southern hemisphere. Members of the *ornata* group are found in warm waters all around the globe. Records of representatives of the *pugio* group are from the southern hemisphere only, from South Africa, South America, and now also from Australia. *A. aequilivestita* is most similar to the African *A. punctata*. The *furcata* group includes psammobiot species; most records are from the Indo-Pacific region, but members of this group are also known from the Black Sea and northeastern Atlantic (Bartsch 1992b).

In the samples from Rottneest Island, there is no representative of the otherwise very common *brevipalpus* group. The lack of records may be due to the small size of Rottneest Island, many habitats are missing (Wells and Walker 1993), and being an area with rather constant environmental parameters such as high salinity and temperature.

Records of the genus *Agauopsis* from southeastern Australia are *A. mokari* and *Agauopsis* sp. (Otto 1994; Bartsch 1985b), both members of the *microrhyncha* group, and *A. collaris* Otto, a representative of the *brevipalpus* group (Otto 1994). The '*Agauopsis brevipalpus*' mentioned in Lohmann (1893) is certainly not conspecific with the northern Atlantic and Mediterranean *A. brevipalpus*. The records of '*Agauopsis microrhyncha*' and '*Agauopsis hirsuta*', listed by Lohmann (1893) from off Sydney, is

thought to be purely a lapse, these species are not included in the systematic part of that publication (Lohmann 1893) and no Australian record is given in Lohmann (1901).

The present knowledge of halacarids from Australian shores represents only scattered bits of information; the number of shore lines visited and habitats surveyed is small. In respect to *Agauopsis*, eastern and western Australia have no co-occurring species. The two species of *Halacaropsis* are sibling but distinct species. It is reasonable to expect distinct faunas in western and eastern shores of southern Australia.

ACKNOWLEDGEMENTS

The material described was collected during the Fifth International Marine Biological Workshop organized by Dr F.E. Wells. His help and that of other participants in the workshop is acknowledged. Thanks are also due to Drs H. Dastych, R.B. Halliday, J. Otto, and R. Smiley for loan of halacarid specimens lodged in the Zoological Museum in Hamburg, the Australian National Insect Collection and the United States National Museum of Natural History.

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Early Cretaceous macrofloras of Western Australia

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Abstract – Western Australian, Lower Cretaceous, macrofloras from the Broome Sandstone and Callawa Formation (Canning Basin), Nanutarra Formation and Birdrong Sandstone (Carnarvon Basin), Cronin Sandstone (Officer Basin), and Leederville and Bullsbrook Formations (Perth Basin) incorporate a range of lycophytes, ferns, pteridosperms, bennettitaleans, and conifers. The new monotypic genus *Roebuckia* is established for spatulate fern fronds (*R. spatulata*) of possible vittariacean alliance. Other newly established species include *Phyllopteroides westralensis*, *Elatocladus ginginensis*, and *Carpolithes bullsbrookensis*. Although the Western Australian fossil suites reveal some specific differences from other Australian late Mesozoic assemblages, several shared index taxa and the high proportion of bennettitaleans support correlation with the Victorian Neocomian *Ptilophyllum*–*Pachypteris austropapillosa* Zone (Zone B). Some Western Australian taxa are shared with Indian assemblages but fewer similarities exist with other Gondwanan Early Cretaceous floras. The representation of several hydrophilous fern, lycophyte, and pteridosperm groups together with growth indices from fossil woods implies a seasonal humid mesothermal climate for the Western Australian cratonic margin during the Neocomian–Barremian. Minor differences between the Western Australian assemblages are attributable to local depositional and preservational factors.

INTRODUCTION

This paper reviews all Western Australian Cretaceous plant fossils held in the collections of the Western Australian Museum and the Department of Geology and Geophysics of the University of Western Australia together with limited material held in the Australian Museum, Sydney. As all specimens lack preserved organic matter, descriptions are based on gross morphology, ornamentation, and venation patterns. This procedure necessarily places limitations on the degree of discrimination between some taxa. However, the scarcity of previous studies on the Western Australian fossil floras invites this systematic appraisal in order to fill some major gaps in the knowledge of Australia's Cretaceous phytogeography.

The relative tectonic stability and deep-weathering associated with much of the central and western part of the Australian continent since the mid-Mesozoic has removed from outcrops most of the organic material required for palynological studies. Apart from scarce vertebrate trackways (Colbert and Merrilees 1967; Long 1990), plant macrofossils are virtually the only fossil remains available in outcrop to date and palaeoenvironmentally categorize Western Australian Cretaceous terrestrial strata. No studies dealing with stratigraphic and petroleum exploration drilling have reported significant

assemblages of plant macrofossils from subsurface Cretaceous strata in Western Australia. Retallack (1977, 1980) and McLoughlin (1993) have illustrated differences in palaeosol development and the composition of plant fossil assemblages in Australian Permian and Triassic strata according to variations in local and regional depositional settings. Such sedimentological and taphonomic controls also apply to the Cretaceous assemblages offering an important tool for detailed interpretation of non-marine sedimentary facies. Additionally, permineralized, mollusc-bored, driftwood preserved in Lower Cretaceous marine sediments has aided the definition of sequence stratigraphic boundaries and systems tracts (McLoughlin *et al.* 1994). Palaeobotanical investigations of the diversity of plant groups together with anatomical indices such as growth ring variation are also useful for the categorization of palaeoclimates and the identification of major food sources available to the large Cretaceous herbivorous dinosaurs.

PREVIOUS STUDIES

Douglas (1969, 1973), Drinnan and Chambers (1986) and McLoughlin *et al.* (1995) have provided the most detailed studies of Australian Cretaceous fossil plants dealing with macrofloras from the Gippsland, Otway and Eromanga Basins. Other

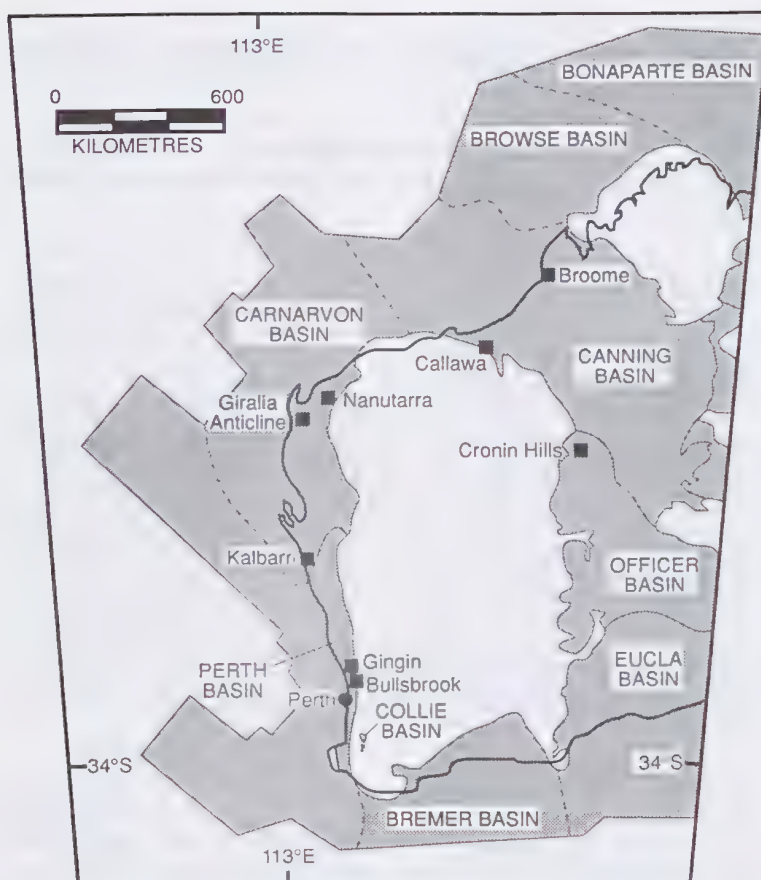


Figure 1 Map of Western Australia showing Phanerozoic sedimentary basins and principal Cretaceous plant macrofossil localities (solid squares).

significant contributions include those of Seward (1904), Chapman (1908, 1909, 1914), Walkom (1918, 1919a), Medwell (1954a,b), Glaessner and Rao (1955), and Dettmann *et al.* (1992). Although several stratigraphic papers have provided lists of fossil plants recovered from Western Australian Cretaceous strata (e.g., Brunnschweiler 1960; Cox 1961; Playford *et al.* 1976) many of these identifications are not supported by illustrations or descriptions and are commonly erroneous. A small assemblage described and illustrated by Walkom (1944) from strata underlying the Molecap Greensand near Gingin is redescribed herein. White (1961a) briefly described and illustrated plant remains recovered from the Canning Basin by Australian Bureau of Mineral Resources regional geological surveys. McLoughlin and Guppy (1993), and McLoughlin and Hill (in press) provided preliminary revised lists of Western Australian Cretaceous plant fossils from several sedimentary basins and briefly discussed some palaeoclimatic implications of the floras.

McLoughlin *et al.* (1994) detailed the anatomical character and palaeoenvironmental significance of silicified and phosphatized woods from the Birdrong Sandstone, Carnarvon Basin and Backhouse *et al.* (1995) described lignitized but anatomically similar woods from the Barremian to earliest Aptian Nakina Formation of the Collie Basin. The Cretaceous palaeobotanical literature from other Gondwanan continents (especially India and South America) is extensive. Therefore, synonymy lists provided here deal only with previously figured or described Western Australian fossil plants.

CRETACEOUS STRATIGRAPHY

Western Australian Cretaceous plant macrofossils have been recovered from the Perth, Carnarvon, Canning, and Officer Basins (Figure 1). Plant remains are best represented in Early Cretaceous non-marine strata (Figure 2). Due to a dearth of palynological studies and the absence of

marine invertebrate biostratigraphic indices, the ages of many of these rock units are only broadly constrained. Furthermore, lack of continuous outcrops in many areas hinders the mapping and lithological correlation of plant-bearing strata and has led to uncertainties over the application of lithostratigraphic names. For example, Playford *et al.* (1976) and Skwarko (1990) assigned Walkom's (1944) Gingin fossil assemblage to the Yarragadee Formation (Middle Jurassic to Tithonian).

However, Feldtman (1963) reported that the plant-bearing horizons occurred within the Strathalbyn Beds, a term which Playford *et al.* (1976) regarded as synonymous with the Leederville Formation. Wilde and Low (1978) also mapped outcrops in the vicinity of Walkom's plant beds (Cheriton Creek) as part of the Leederville Formation. On the basis of lithology and stratigraphic position, the fossils are here regarded as belonging to the marine to continental Leederville Formation (Hauterivian–

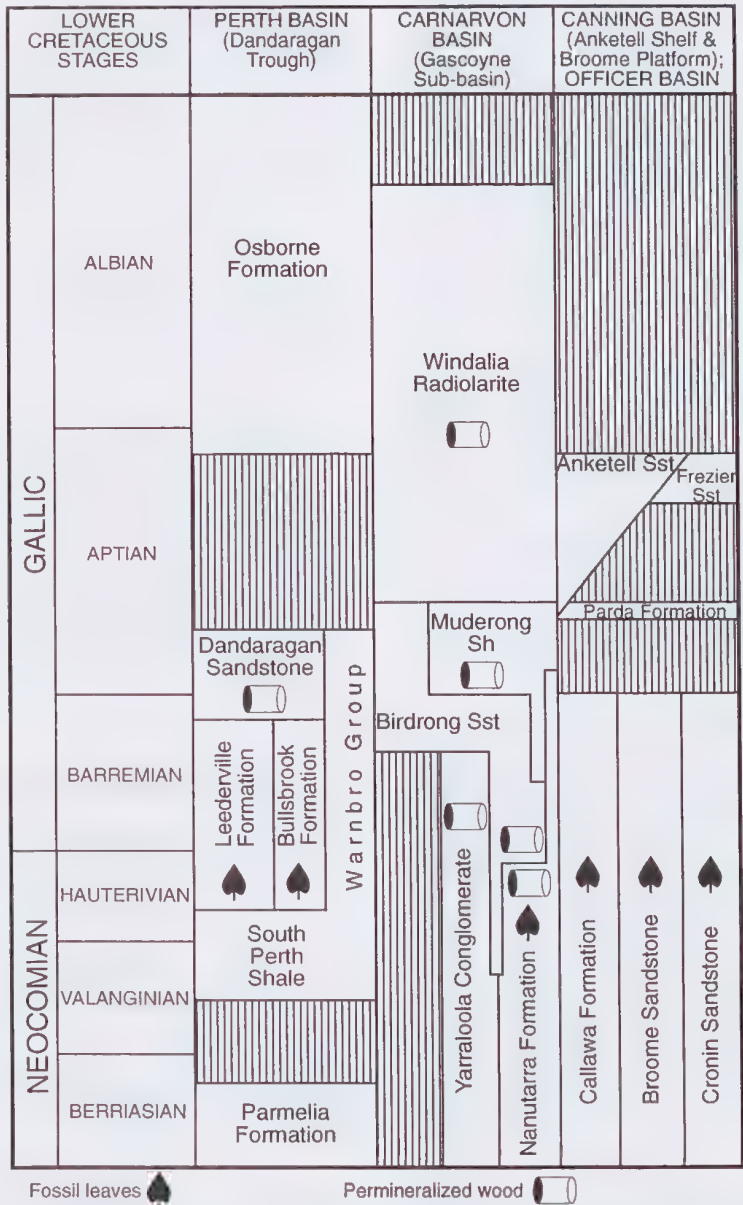


Figure 2 Stratigraphic correlation of Lower Cretaceous rock units in the Perth, Carnarvon, and Canning Basins, Western Australia (after Cockbain 1990; Hocking 1990; Middleton 1990) showing the distribution of plant macrofossil assemblages.

Barremian): Figure 2. The Bullsbrook Formation, exposed 2 km east of Bullsbrook, is a fully continental lateral equivalent of the Leederville Formation (Figure 2).

The Neocomian–?Aptian shallow marine to paralic Birdrong Sandstone is chiefly exposed along the Murchison River near Kalbarri, on the flanks of the Kennedy Ranges, and in the Giralda Anticline within the Carnarvon Basin (Hocking *et al.* 1987; McLoughlin *et al.* 1994). The upper part of this unit is typically rich in fragmentary permineralized gymnosperm wood showing evidence of intensive molluscan borings. Other Cretaceous marine units in the Carnarvon Basin contain sparse fossil woods, and leaf impressions occur within the paralic Nanutarra Formation near the Ashburton River (Figure 1). Lignified wood is also locally preserved in the Lower Cretaceous Nakina Formation, Collie Basin, in the state's southwest (Backhouse *et al.* 1995).

The Broome Sandstone of the northern Canning Basin was deposited within deltaic to shallow marine environments whereas the laterally equivalent Callawa Formation in the basin's southwest is fluvial in origin (Towner and Gibson 1983). The coeval Cronin Sandstone, outcropping in the northwestern part of the contiguous Officer Basin (Figures 1,2) was also laid down in fluvial environments (Towner and Gibson 1983). These plant-bearing units have been regarded as Late Jurassic to Early Cretaceous or even fully Jurassic on the basis of previous phytostratigraphic interpretations (Middleton 1990). However, a Neocomian–Barremian age for the plant-bearing portions of these units is proposed herein based on revised fossil identifications.

MATERIAL AND METHODS

The majority of material described and figured in this study is held in the collections of the Western Australian Museum (specimens prefixed WAM) and the Department of Geology and Geophysics, University of Western Australia (specimens prefixed UWA). Counterparts of some of Walkom's (1944) specimens are lodged with the Australian Museum in Sydney (specimens prefixed AMF). The Commonwealth Palaeontological Collection housed by the Australian Geological Survey Organisation, Canberra, contains limited Canning and Officer Basin material from regional geological surveys of the 1950s and 60s and has been illustrated by White (1961a). The latter material was not re-examined during this study but in most cases White's (1961a) illustrations are adequate for identification purposes and her studied specimens are systematically discussed herein.

All descriptions are based on impression fossils

preserved in ferruginous shale and medium-grained quartzose sandstone apart from some seeds, megaspores, and axes which are preserved as natural clay or sandstone casts. Organic material was not preserved on any fossils but in some cases latex and silicone casts yielded morphological details not clearly evident on negative impressions. All specimens were illustrated under strong unilateral light directed from the upper left unless otherwise stated.

Fossil localities are as follows:

- Broome Sandstone – Gantheaume Point, Broome (material collected by W.H. Butler, A. Dawson, I. and T. Foulkes, J. Long, D. and M. Merrilees, J. Pas, G. Zeck); Quandong Beach, 10 km north of Broome lighthouse (material collected by I.M. Doust).
- Nanutarra Formation – Cited as "6.5 km north of Globe Hill, Ashburton River" on specimen labels (material collected by D.W. McLeod). This is probably the plant fossil locality 2.5 km north of the junction of Jubricoo Creek and Ashburton River, 8 km west of Nanutarra indicated by van de Graaf *et al.* (1980).
- Birdrong Sandstone – Near Toolonga Hill (114°16'6"E 27°34'3"S), Murchison House Station, 10 km northeast of Kalbarri (material collected by S. McLoughlin); 1 km northwest of Black Dam (114°10'9"E 23°6'3"S), Cardabia Station, 35 km east of Coral Bay (material collected by D.W. Haig, R. Howe, G. Ellis, S. McLoughlin).
- Leederville Formation – Cheriton Creek, about 500 m east of MacIntyre Gully, 2.5 km north of Gingin (material collected by E. de C. Clarke).
- Bullsbrook Formation – 2.5 km northeast of Bullsbrook Hotel (material collected by A. Page).

SYSTEMATIC PALAEOBOTANY

Division Lycophyta

Class Lycopsidea

Order Isoetales

Family Isoetaceae

Genus *Isoetites* Münster, 1842

Type species

Isoetites crociformis Münster, 1842; Jurassic; Daiting near Manheim, Germany.

Isoetites elegans Walkom, 1944 Figures 3A, C–F

1944 *Isoetites elegans* Walkom; p. 202; plate 1, figs 1–5.

1986 Megasporangia of *Isoetes*; White; p. 169; figure 260.

1993 *Isoetites elegans*; McLoughlin and Guppy; p. 14; figure 12.

Holotype

UWA16687; Leederville Formation (Neocomian–Barremian), Perth Basin, Western Australia (Walkom 1944).

Material

UWA16682, UWA16683 (principal sporangia-bearing specimen), UWA16684, UWA16685, UWA16687 (principal foliage-bearing specimen), UWA16690, UWA16703, UWA16711. Counterparts of some specimens are held in the Australian Museum (AMF39815: see White 1986, figure 260).

Distribution

Leederville Formation (Neocomian–Barremian), Perth Basin, Western Australia. Previous assignation of these specimens to the Jurassic (Walkom 1944; Ash and Pigg 1991) is now deemed erroneous.

Description

Numerous (>30) radiating linear leaves, reaching at least 10 cm long, 5 mm wide, bases not preserved, apices pointed, margins entire (Figure 3A). Longitudinal striae evident on some leaves but venation otherwise indistinct. Associated megasporophylls on type locality slabs bear clusters of numerous (>30) trilete megasporangia. Megasporophylls identical to sterile leaves, showing no expansion around sporangia. Megasporangia reach 10 mm long, 2.5 mm wide (Figure 3C). Megasporangia 0.5 mm in diameter, circular in polar compression, laesurae prominent; contact surfaces extending almost to the equator, laevigate; distal surface reticulate (moulds coarsely granulate: Figure 3D). Associated microsporophylls bear elliptical microsporangia, 10 mm long, 3 mm wide, consisting of densely matted casts of ill-defined microspores (Figures 3E,F).

Comments

Although the earliest records of *Isoetites* are from the Upper Triassic (Bock 1962), they underwent a phase of global diversification during the Early Cretaceous (Pigg 1992). Ash and Pigg (1991) listed the fossil species previously assigned to *Isoetites* Münster 1842 and *Isoetes* Linnaeus 1753. All examples essentially consist of linear leaves or sporophylls either in isolation or attached in rosettes to short cylindrical or spherical corms. Other species can be distinguished from *I. elegans* by possession of serrate leaf margins (*Isoetites serratus* Brown, 1939, *Isoetites serratifolius* Bose and

Roy, 1964), air channels within the leaves (*Isoetites horridus* (Dawson) Brown, 1939), the details of megasporangia and cuticle (*Isoetites choffati* Saporta, 1894, *Isoetes reticulata* Hill, 1987), leaf proportions (*Isoetites gramineoides* Bock, 1962, *Isoetites rolandii* Ash and Pigg, 1991), and corm dimensions (*Isoetites crociformis* Münster, 1842, *Isoetites circularis* (Emmons) Brown, 1958).

Isoetes janaianus Banerji, 1989 from the Middle to Upper Jurassic of India has similar leaves and sporangia to *I. elegans* but is characterized by a 5-lobed rhizomorph whereas corms are not yet available for the latter species. *Isoetites bulbiformis* Drinnan and Chambers, 1986 from the Victorian Lower Cretaceous, distinguished by its smaller size and expanded leaf tips, may represent gymnospermous remains. The Indian Lower Cretaceous *Isoetites indicus* Bose and Roy, 1964, although represented only by sporophyll bases, is characterized by its smaller but more numerous megasporangia (Bose and Banerji 1984).

Genus *Nathorstianella* Glaessner and Rao, 1955

Type species

Nathorstianella babbagensis (Woodward) Glaessner and Rao, 1955; Lower Cretaceous; Mt Babbage, South Australia.

Nathorstianella babbagensis (Woodward) Glaessner and Rao, 1955

Figure 3B

cf. 1961 "fragment of stem" White; p. 304; plate 6, figure 3. [1961a].

Holotype

F15070 (Adelaide University Geology Department); Algebuckina Sandstone (Neocomian); Mt Babbage, South Australia (Glaessner and Rao 1955).

Material

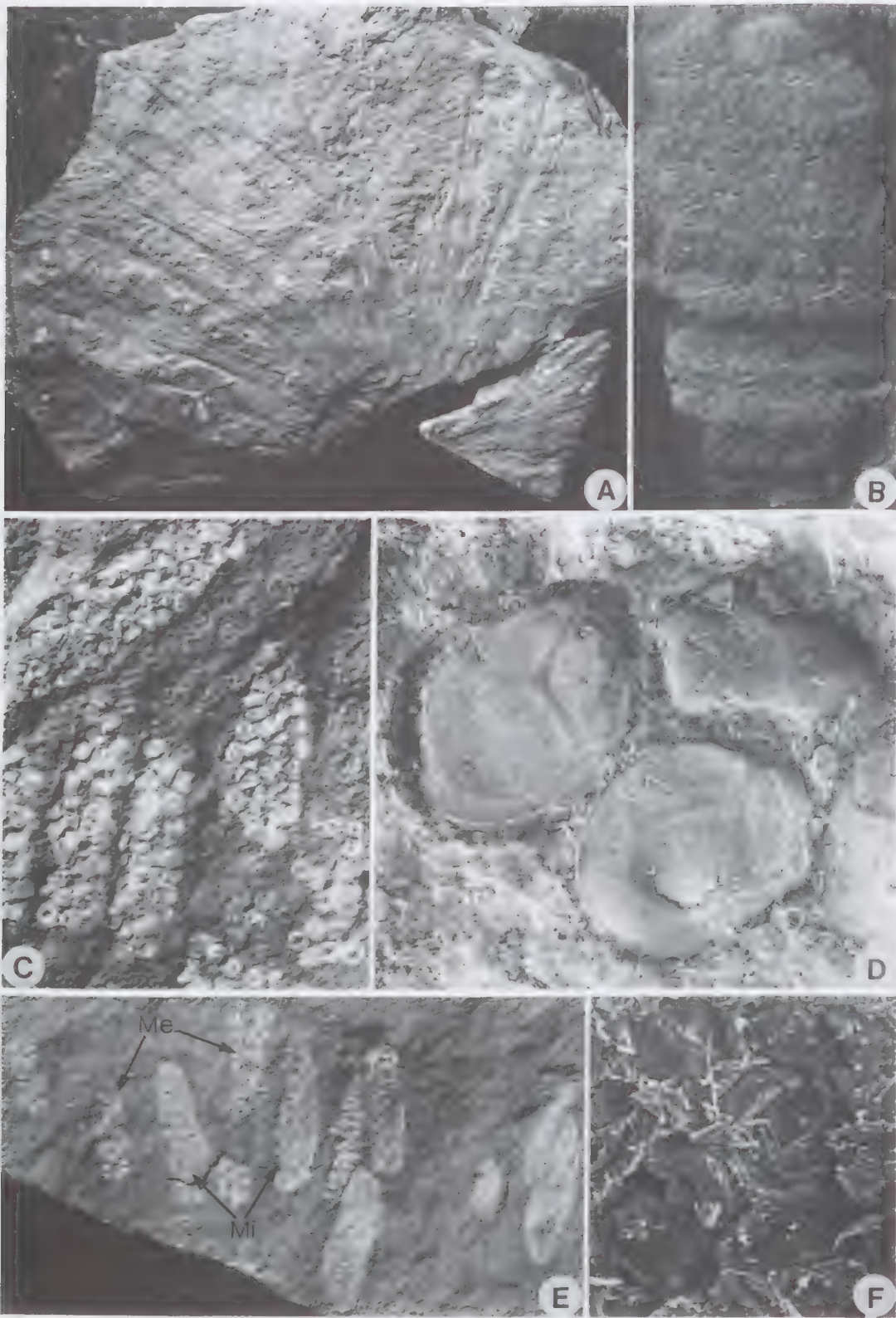
WAM P.88.2, WAM P.96.12.

Distribution

Algebuckina Sandstone (Berriasian–early Valanginian), Eromanga Basin, South Australia (Dettmann *et al.* 1992); Broome Sandstone (Neocomian–Barremian), Canning Basin, Western Australia (this study).

Description

Fragmentary casts of cylindrical axes (14–17 mm wide, 24–35 mm long) bearing numerous spirally arranged leaf or root scars (Figure 3B). Scars diminutive (0.5 mm wide, 0.25 mm high), c. 0.5–1



mm apart, arranged in flat (70°–75°) right-handed and steep (50°) left-handed spirals (measured with respect to axial orientation). Axes show broad transverse ridges or undulations corresponding to growth increments. Attached roots unavailable. Leaves unavailable on curated specimens.

Comments

Glaessner and Rao (1955) suggested a possible relationship between leafless *Nathorstianella* corms and foliage assigned to *Isoetes elegans*. Leaves 4 mm wide, 60 mm long and similar to *I. elegans*, but lacking sporangia, were observed attached to *N. babbagensis* axes in outcrops of the Broome Sandstone at Gantheaume Point near Broome during this study. The specimens are preserved in rock slabs too large to be collected or extracted without risking damage to the fossils. It seems likely that *I. elegans* leaves and *N. babbagensis* belonged to the same plant although formal synonymy should wait until fertile material is found attached to the latter. The occurrence of *N. babbagensis* in sandy deltaic sediments of the Broome Sandstone suggests that this plant preferred coastal habitats similar to those occupied by related herbaceous to arborescent Triassic pleuromeian lycophytes (Retallack 1977; Karrfalt 1986).

Division Pteridophyta

Class Filicopsida

Order Filicales

Family Dipteridaceae

Genus *Hausmannia* Dunker, 1846

Type species

Hausmannia dichotoma Dunker, 1846; Jurassic; near Buckenburg, Bavaria.

Hausmannia sp.

Figures 4A,C

1961 *Hausmannia* sp.; White; p. 306; plate 8, figure 4. [1961a].

1993 *Hausmannia* sp.; McLoughlin and Guppy; p. 14; figure 7.

Material

WAM P.65.42, WAM P.88.13, WAM P.89.166, WAM P.89.181, WAM P.96.9.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin; Lees Sandstone (Neocomian?), Carpentaria Basin, Northern Territory (White 1961b; Dettmann *et al.* 1992).

Description

Frond flabellate, up to 42 mm long and 47 mm wide; base cuneate, tapering to long petiole (Figure 4C); apex rounded, undulate, or broadly dentate. Single vein enters base of frond from petiole, bifurcates up to six times producing a radiating array of dominant veins; each ultimate dominant vein enters base of a marginal tooth (Figure 4A). Up to five orders of closely anastomosing subsidiary veins subdivide lamina between dominant veins into a meshwork of <0.25 mm² aureoles. Petiole 1 mm wide, >6.5 cm long. Sporangia not evident.

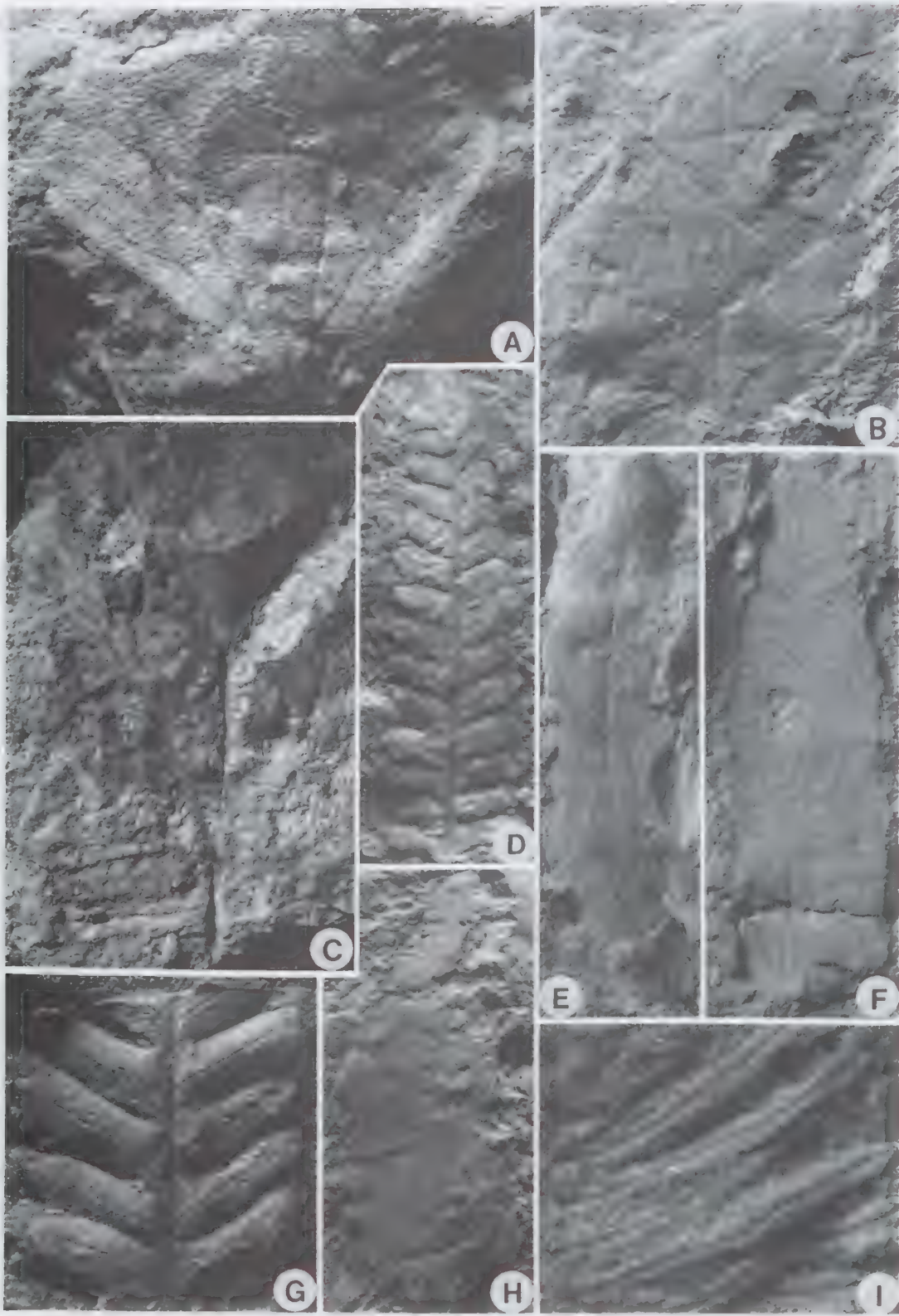
Comments

Hausmannia has affinities with reticulate-veined pinnatifid dipteridacean fronds such as *Goepfertella* Oishi and Yamashita emend. Arrondo and Petriella, 1982, *Dictyophyllum* Lindley and Hutton, 1834, *Thaumatopteris* Goepfert, 1841, and *Clathropteris* Brongniart, 1828 (Herbst, 1975). *Hausmannia* had a cosmopolitan distribution during the Jurassic and Cretaceous (Corsin and Waterlot 1979) with several species known from gondwanan continents, although some are based on scanty material.

Hausmannia papilio Feruglio emend. Herbst 1960 fronds from the Early Cretaceous of Argentina are most closely comparable to the Western Australian specimens although examples of the former do not show long petioles and are more circular with slightly auriculate bases (Herbst 1960). *Hausmannia pachyderma* Sukh-Dev 1972b and specimens assigned to *Hausmannia crenata* (Nathorst) Möller from India (Bose and Sah 1968) can be distinguished from the Western Australian form by their undulate margins and coarsely reticulate venation. The Indian *H. crookshanki* Shah and Singh, 1964 differs by its apically cleft lamina.

Of the previously described Australian

◀ **Figure 3** A *Isoetes elegans* Walkom 1944; Rosette of linear univeined leaves; UWA16687; Leederville Formation; x 0.8; B, *Nathorstianella babbagensis* (Woodward) Glaessner and Rao, 1955; Corm impression with spirally arranged leaf/root scars; WAM P.88.2; Broome Sandstone; x 3; C, Megasporangia of *Isoetes elegans* Walkom, 1944; UWA16683; Leederville Formation; x 8; D, Scanning electron micrograph of *Isoetes elegans* Walkom, 1944 megaspores; AMF39815; Leederville Formation; x 100; E, Microsporangia (Mi) and megasporangia (Me) of *Isoetes elegans* Walkom, 1944; UWA16683; Leederville Formation; x 4; F, Scanning electron micrograph of surface of *Isoetes elegans* Walkom, 1944 microsporangium showing ill-defined microspore outlines; AMF39815; Leederville Formation; x 1000.



Hausmannia species, Herbst (1979) considered that only *H. wilkinsii* Walkom, 1928, *H. sp. cf. H. defarrariisii* Feruglio, 1937, and *H. bulbaformis* Douglas, 1973 were distinguishable. *Hausmannia wilkinsii* and *H. bulbaformis* are both differentiated from the Western Australian form by their strongly dissected lamina (Walkom 1928; Douglas 1973). *Hausmannia sp. cf. H. defarrariisii* from the Middle Jurassic Walloon Coal Measures (Herbst 1979; McLoughlin and Drinnan 1995) differs by its pronounced apical lamina incision and auriculate base with respect to both Northern Territory fronds illustrated by White (1961b, 1966) and the forms from the Broome Sandstone. It is likely that both the Northern Territory and Western Australian Early Cretaceous forms are conspecific.

Order Osmundales

Family Osmundaceae

Genus *Cladophlebis* Brongniart, 1849

Type species

Cladophlebis albertsii (Dunker) Brongniart, 1849; ?Jurassic; Germany.

Cladophlebis sp. cf. C. oblonga Halle, 1913
Figures 4B,D,G

1961 *Cladophlebis australis* (Morris); White; p. 304; plate 7, figures 1, 6. [1961a].

1993 *Cladophlebis sp. cf. C. oblonga*; McLoughlin and Guppy; figure 2.

Material

WAM P.64.5, WAM P.65.40, WAM P.88.9, WAM P.88.10, WAM P.88.12.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin; Algebuckina Sandstone, South Australia (all Lower Cretaceous).

Description

Fronds pinnate or bipinnate (imparipinnate). Rachis prominent, striate, <1.5 mm wide, gently tapering distally. Pinnules alternate, oblong, up to

6 mm wide, 18 mm long; apex rounded to obtusely pointed, margin entire, basiscopic margin straight or convex, acroscopic margin straight (Figures 4B,D). Adjacent pinnule bases contiguous. Pinnules arise at c. 50° from rachilla. Pinnules have alethopteroid venation; veins depart pinnule midrib at 50°–60°, bifurcate once or twice, pass straight to margin, no anastomoses (Figure 4G). Pinnule midribs evanescent c. 3 mm before apex.

Comments

Cladophlebis foliage is abundant and widespread in Permian to Cainozoic strata throughout the world. Many species referred to this genus have been assigned to the Osmundaceae based on the possession of osmundaceous sporangia and spores or by association with permineralized osmundaceous axes. Specimens lacking attached axial or fertile remains are assigned to a large array of form species based on frond and pinnule shape and venation patterns. The variation of pinnule shapes evident on different parts of some extant fern fronds suggests that description of inadequate material may have led to a proliferation of names for *Cladophlebis* species.

Australian cladophlebid fronds from a wide range of localities and ages have been commonly assigned to *Cladophlebis australis* (Morris) Seward, 1904, a species originally erected for Triassic fronds from Tasmania (Morris 1845). The variation in Australian *C. australis* pinnule shapes appears to be roughly equivalent to the range evident between the many South American species (Herbst 1971). Morris's (1845) original illustrations of *C. australis* show slender tapering falcate pinnules quite different from the Western Australian form described here. The studied specimens are compared with *C. oblonga* Halle, 1913 based on their relatively oblong pinnules with rounded or weakly pointed apices although some Antarctic and South American examples of this species have slightly shorter and more falcate pinnules than the Western Australian forms (Halle 1913; Herbst 1971; Arrondo and Petriella 1980). Though poorly preserved and slightly smaller, White's (1961a) oblong *Cladophlebis australis* pinnae from the Callawa Formation appear to be conspecific with the Broome and Bullsbrook fronds as are the South Australian specimens of Glaessner and Rao (1955).

◀ **Figure 4** **A**, *Hausmannia sp.*; WAM P.88.13; Broome Sandstone; x 2; **B**, *Cladophlebis cf. oblonga* Halle, 1913; UWA10465A; Bullsbrook Formation; x 2; **C**, *Hausmannia sp.*; Two fragmentary fronds with long slender rachises; WAM P.89.181; Broome Sandstone; x 1; **D**, *Cladophlebis cf. oblonga* Halle, 1913; Pinna with preserved apex; WAM P.88.12; Broome Sandstone; x 1.5; **E,F,H**, Isolated pinnules of *Phyllopteroides westralensis sp. nov.*; (E) UWA10473, (F) UWA10473, (H) UWA10467C; Bullsbrook Formation; all x 3; **G**, *Cladophlebis cf. oblonga* Halle, 1913 showing details of venation; WAM P.88.9; Broome Sandstone; x 2; **I**, *Microphylopteris gleichemoides* (Oldham and Morris) Walkom 1919a; Enlargement showing details of pinnae; WAM P.88.1; Broome Sandstone; x 3.

Walkom's (1919a) Early Cretaceous *C. australis* specimens from Queensland are also comparable in terms of pinnule shape but appear to have more prominent, but less divided, secondary veins. The Western Australian fronds have similarly proportioned pinnules and venation patterns to *Cladophlebis* sp. cf. *C. oblonga* Halle, 1913 of Drinnan and Chambers (1986) although the Victorian examples have more sharply acute apices.

The oblong shape and generally rounded pinnule apices of the Western Australian specimens distinguish them from many of the Indian Mesozoic *Cladophlebis* species which typically have either shorter elliptical or more narrow and elongate (lanceolate to falcate) pinnules often with acutely pointed apices (Bose and Sah 1968; Sukh-Dev 1972a; Zeba-Bano 1980; Roy 1968; Bose and Banerji 1984; Kasat 1970).

Herbst (1971) reviewed South American Mesozoic fronds assigned to 17 *Cladophlebis* species. Of these, *C. denticulata* Brongniart, 1828 and *C. patagonica* Frenguelli, 1947 have similarly sized oblong pinnules to the Western Australian specimens but are distinguished by their prominently pointed acute apices (Baldoni 1980a; Longobucco *et al.* 1985). The Western Australian specimens compare favourably to Archangelsky's (1964b) *Cladophlebis* sp., *C. oblonga* Halle, 1913, *C. pintadensis* Herbst, 1966, and *C. haiburnensis* var *rectimarginata* Herbst, 1966 and it appears that few individual features enable consistent differentiation of these species in the absence of fertile or cuticular material.

South African Early Cretaceous *Cladophlebis bezuidenhoutensis* Gianniny and Wiens and *C. dunbrodiensis* Gianniny and Wiens (in Anderson and Anderson, 1985) fronds clearly differ from the Western Australian form by their undulate pinnule margins. Other South African species differ by their smaller, more elongate, contracted or falcate pinnules (Anderson and Anderson 1985).

Genus *Phyllopteroides* Medwell, 1954b

Type species

Phyllopteroides dentata Medwell, 1954b; Early Cretaceous; Killara, Otway Basin, Victoria.

Phyllopteroides westralensis sp. nov.

Figures 4E,F,H; 5A

1961 *Linguifolium denmeadi* Jones and de Jersey; White; p. 302; plate 5, figure 3. [1961a].

1993 *Phyllopteroides lanceolata*; McLoughlin and Guppy; figures 4, 11.

Holotype

UWA10473C (Figure 5A); Bullsbrook Formation

(Neocomian–Barremian); Bullsbrook, Perth Basin, Western Australia.

Etymology

Signifying the Western Australian distribution of the species.

Material

WAM P.96.11. UWA10461D, UWA10462A, UWA10464A, UWA10467C, UWA10470A–B, UWA10472A, UWA10473B–D, E–F, UWA10474C.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin; Cronin Sandstone, Officer Basin (all Neocomian–Barremian).

Diagnosis

Fronds imparipinnate; pinnules narrowly elliptical to lanceolate, base tapering acute with short petiolule, apex rounded, margin entire or gently undulate; secondary veins once or twice dichotomous, 15–20 veins per cm, intersecting margin at 20°–40°.

Description

Fronds pinnate (imparipinnate). Rachis slender (<2 mm) wide. Pinnules narrowly elliptical to lanceolate, reaching 10 mm wide, 40 mm long, inserted alternately on rachis at c. 40° (Figure 5A). Base tapering acute, joined to rachis by short (<2 mm petiole), apex rounded, margin entire or gently undulate. Pinnules show weakly defined evanescent midrib. Secondary veins once or twice dichotomous, arch gently from indistinct midvein to intersect margin at 20°–40°, 15–20 veins per cm; no anastomoses (Figures 4E,F,H).

Comments

Cantrill and Webb (1987) re-evaluated the genus *Phyllopteroides* and indicated its likely affinity to the Osmundaceae based on the association of sterile *P. dentata* fronds with osmundaceous sporangiate remains (*Caecumen expansa* Cantrill and Webb, 1987). Five species (viz., *P. dentata* Medwell, 1954b, *P. lanceolata* (Walkom) Medwell, 1954b, *P. serrata* Cantrill and Webb, 1987, *P. laevis* Cantrill and Webb, 1987, and *P. macclymontae* McLoughlin, Drinnan and Rozefelds, 1995) have been described from Australia. The entire-margined lanceolate Western Australian leaves compare most closely with *P. lanceolata* identified from Albian strata of central Queensland (Walkom 1919a). However, *P. westralensis* sp. nov. differs by its consistently entire pinnule margins, substantially lesser venation angle, and generally lesser vein densities. *Phyllopteroides dentata*, *P. serrata* and *P. macclymontae* can be distinguished by their strongly

dentate or serrate margins. *Phyllopteroides laevis* leaflets may also have entire margins, however, they differ from *P. lanceolata* by their more broadly elliptical shape. White's (1961a) *Linguifolium denmeadi* from the Cronin Sandstone, Officer Basin, is here regarded as a detached *P. westralensis* pinnule.

Cantrill and Webb (1987) suggested that the successive stratigraphic ranges of *P. laevis*, *P. serrata*, and *P. dentata* in Victoria represented elements of an evolutionary lineage. They also suggested that the Queensland *P. lanceolata* arose from the same Neocomian–Aptian stock but evolved independently of the Albian *P. dentata* of Victoria. The Neocomian–Barremian *P. westralensis* may represent a separate lineage derived from entire-margined *P. laevis* stock which became restricted to the lowlands of the continent's western margin. Few fossil fronds outside Australia are comparable with *P. westralensis* although *Thinnfeldia chunakhalensis* Sah and Sukh Dev, 1958 may be referable to *Phyllopteroides* based on its *P. laevis*-like pinnules.

Order Gleicheniales

Family Gleicheniaceae

Genus *Microphylopteris* Arber, 1917

Type species

Microphylopteris pectinata (Hector) Arber, 1917; Lower Jurassic; Mataura Falls, New Zealand.

Microphylopteris gleichenioides
(Oldham and Morris) Walkom, 1919a
Figures 4I; 5B

1993 *Microphylopteris gleichenioides*; McLoughlin and Guppy; figures 5, 6.

Lectotype

No. 4444 (Geological Survey of India, Calcutta); Rajmahal Series (?Lower Cretaceous), Rajmahal Hills, India. Selected by Bose and Sah (1968).

Material

WAM P.88.1.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin; Dalrymple Sandstone (Upper Jurassic), Laura Basin, Queensland (Walkom 1928); Burrum Coal Measures (Albian), Maryborough Basin, Queensland (Walkom 1919a); Rajmahal Series and equivalents (Lower Cretaceous) of Peninsula India (Seward and Sahni 1920; Bose and Sah 1968).

Description

Frond at least bipinnate (Figure 5B). Rachis slender (<2 mm wide). Pinnae linear, opposite to subopposite, arched distally, up to 2.5 mm wide, 30 mm long, inserted on rachis at 70°–90°. Pinnules minute (1 × 1 mm), showing full basal attachment, semicircular, alternate, apices rounded (Figure 4I). No sporangia evident.

Comments

Arber (1917) established *Microphylopteris* for fronds resembling extant *Gleichenia* ferns but lacking definitive evidence for a relationship to that genus. However, many workers have continued to assign such fronds to *Gleichenites* Goeppert, 1836 or *Gleichenia* Smith, 1793 even in the absence of fertile material. *Microphylopteris gleichenioides* (Oldham and Morris) Walkom 1919a and comparable forms have been reported from Upper Jurassic to mid-Cretaceous strata in Queensland (Walkom 1919a, 1928; McLoughlin *et al.* 1995). *Gleichenites nanopinnatus* (Douglas) Drinnan and Chambers 1986 from the Lower Cretaceous of Victoria has larger and more dissected pinnules than *M. gleichenioides*.

Gleichenites sp. of Arrondo and Petriella (1980) from the Argentinian Jurassic is a much larger frond than *M. gleichenioides* but has similar pinnules and may be closely related to the Australian species. *Gleichenites sanmartinii* Halle emend. Herbst 1962a and *G. vegagrandis* Herbst, 1962a from the Cretaceous of Argentina and Antarctica also have similar diminutive semicircular pinnules although these are slightly inclined distally (Herbst 1962a, b).

Some Indian examples of '*Gleichenites gleichenioides*' and *Microphylopteris* sp. illustrated by Sah (1965) and Bose and Sah (1968) differ slightly from the Australian *M. gleichenioides* in having pinnules which are strongly deflected towards the pinna apex (insertion angle about 60°).

Order ?Pteridales

Family ?Vittariaceae

Roebeckia gen. nov.

Type species

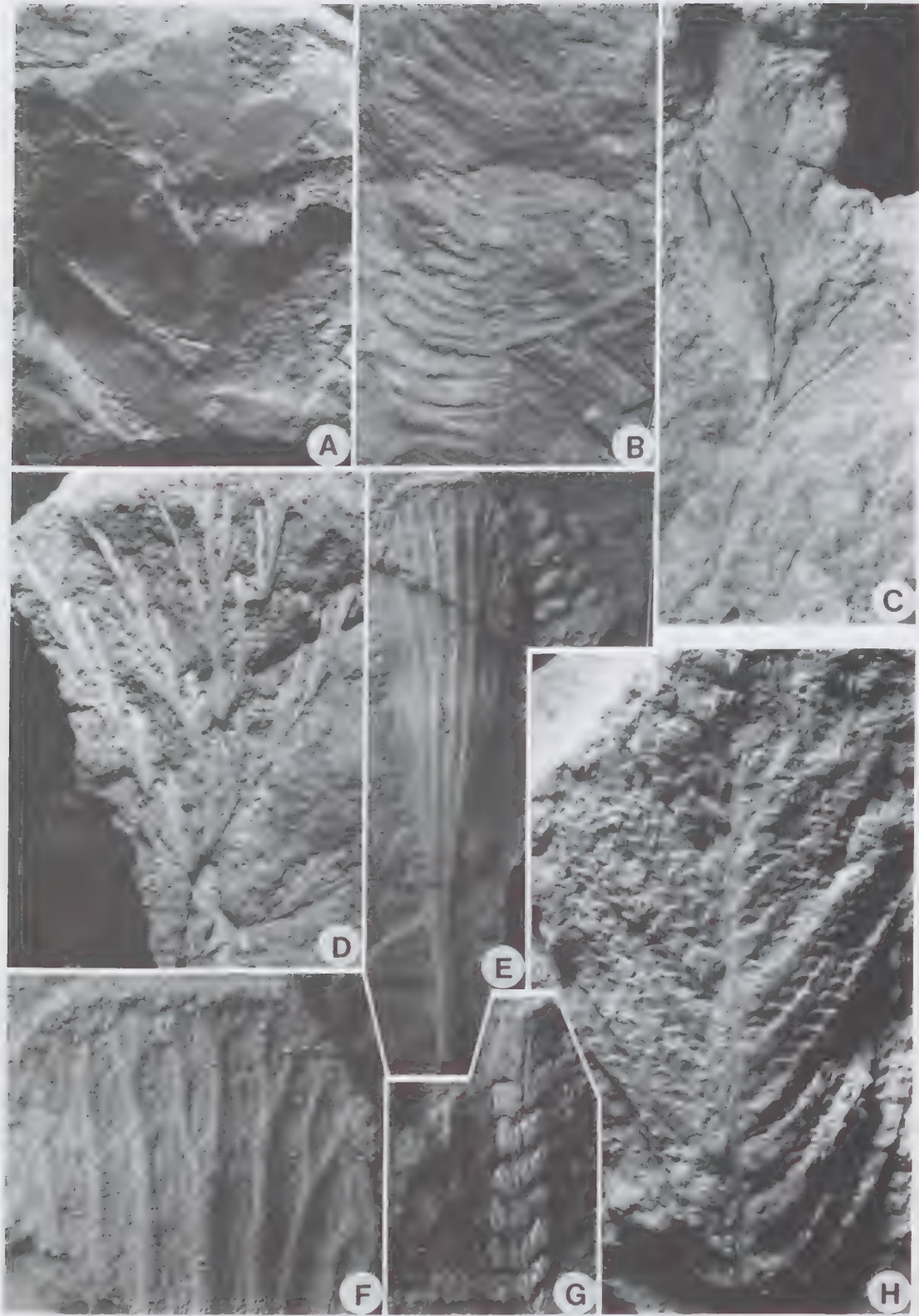
Roebeckia spatulata sp. nov.; Broome Sandstone (Neocomian–Barremian); Gantheaume Point, Broome, Canning Basin, Western Australia.

Diagnosis and discussion

See under *Roebeckia spatulata* below.

Distribution

Known only from the type formation.



Roebuckia spatulata sp. nov.

Figures 5E,F

1993 Indeterminate spatulate frond; McLoughlin and Guppy; p. 14; figure 9 (lower part).

Holotype

WAM P.88.15 (Figures 5E,F); Broome Sandstone (Neocomian–Barremian); Gantheaume Point, Broome, Canning Basin, Western Australia.

Etymology

Genus: after Roebuck Bay near Broome. Species: denoting frond shape.

Material

WAM P.88.15.

Distribution

Broome Sandstone (Neocomian–Barremian); Canning Basin.

Combined diagnosis for genus and species

Frond oblanceolate, margin entire, apex rounded, base acute, petiolate. Single robust vein in petiole, repeatedly dichotomous and gently divergent across lamina. Veins terminate at apex or distal part of lateral margin. Longitudinally elliptical sori inserted in depressions and arranged in 1–2 rows between each pair of veins on distal portion of frond.

Description

Single available spatulate frond 13 mm wide, 56 mm long. Frond margin entire, apex rounded, base tapering acutely to a 15 mm long petiole (Figure 5E). Single vein emerges from base, bifurcates up to five times. Veins gently diverge distally, terminating at apical margin or distal part of lateral margin; no anastomoses, no marginal vein. Sori impressions evident on distal portions of leaf (best seen on latex cast). Sori elliptical, inserted in depressions, reaching 0.5 mm wide, 2 mm long, arranged in 1–2 rows between adjacent veins (Figure 5F). Sori have granular appearance (on casts) but details of sporangia or spores unavailable.

Comments

Although only a single leaf of the type species is known, the specimen is deemed sufficiently distinctive to warrant the erection of a new genus

and species. Superficially, the specimen resembles a ginkgophyte leaf in terms of its divergent dichotomous venation. However, Mesozoic ginkgophytes typically have broadly flabellate, leaves with much finer and more closely spaced venation (Sah 1952, 1953; Baksi 1968; Mehta and Sud 1953; Sah and Jain 1965; Bose 1958; Bose and Sukh Dev 1960; Anderson and Anderson 1989).

The Broome Sandstone specimen is clearly a pteridophyte owing to the presence of rows of elliptical sori between the ultimate veins. Species of the extant tropical epiphytic or lithophytic vittariacean fern genus *Antrophyum* Kaulfuss, 1824 have pendant spatulate fronds similar to *Roebuckia* but their veins are commonly reticulate with flanking dichotomous or reticulate sori (Clifford and Constantine 1980; Piggott 1988). *Roebuckia spatulata* resembles individual oblanceolate pinnules of *Adiantopteris oshimaensis* Kimura, Ohana and Aiba 1990 but is a larger leaf with more robust and less dense venation.

Incertae sedis**Genus *Aculea* Douglas, 1973****Type species**

Aculea bifida Douglas, 1973; Lower Cretaceous; Boola Boola Forest; Victoria.

***Aculea bifida* Douglas, 1973**

Figure 5D

cf. 1961 *Stenopteris tripinnata* (Walkom); White; p. 302; plate 4, figure 6. [1961a].

Holotype

GSV60879 (Geological Survey of Victoria), Strzelecki Group, Zone B (Neocomian); Boola Boola Forest, Gippsland, Victoria.

Material

UWA120489.

Distribution

Strzelecki Group, Zones B–C (Neocomian–Aptian), Gippsland Basin, Victoria (Douglas 1973); Broome Sandstone (Neocomian–Barremian), Canning Basin, Western Australia.

◀ **Figure 5** A, *Phyllopteroides westralensis* sp. nov.; Portion of frond; UWA10473C; Bullsbrook Formation; $\times 1.5$; B, *Microphylopteris gleichenioides* (Oldham and Morris) Walkom 1919a; WAM P.88.1; Broome Sandstone; $\times 1$; C, *Sphenopteris warragulensis* McCoy (in Stirling), 1892; WAM P.89.176; Broome Sandstone; $\times 1$; D, *Aculea bifida* Douglas 1973; UWA120489; Broome Sandstone; $\times 2$; E, Latex cast of *Roebuckia spatulata* gen. et sp. nov., WAM P.88.15 (left) overlying a fragmentary *Bucklandia* sp. axis with spiral rhomboid leaf scars, WAM P.96.8 (upper right); Broome Sandstone; $\times 2$; F, Enlargement of distal portion of latex cast of *Roebuckia spatulata* frond showing elliptical sori between veins; WAM P.88.15; $\times 6$; G, *Sphenopteris* sp. A; WAM P.89.186; Isolated pinna; Broome Sandstone; $\times 2$; H, *Sphenopteris* sp. A; WAM P.89.167; Broome Sandstone; $\times 1$.

Description

Bipinnate, probably elliptical to rhomboid-shaped frond. Rachis slender (<1 mm wide) with prominent central longitudinal ridge (on impressions). Pinnae lanceolate, reaching 6 mm wide, 35 mm long, departing rachis at 20°–25°, alternate. Pinnules, needle-like or slightly flattened (Figure 5D), sub-opposite to alternate, <1 mm wide, reaching 12 mm long, with single median vein persisting to apex; base decurrent, apex pointed acute.

Comments

Although only a single sterile frond portion is available from the Broome Sandstone, it shows the deeply dissected lamina and univeined linear pinnules typical of Early Cretaceous Victorian examples of *Aculea bifida* (Douglas 1973; Drinnan and Chambers 1986). Dissected foliage of this type had previously been assigned to *Sphenopteris* or *Stenopteris* species (Seward 1904; Chapman 1909). White's (1961a) *Stenopteris tripinnata* (Walkom) from the Cronin Sandstone is comparable to *A. bifida* although her figured specimen appears to have more numerous pinnules arranged in a more regular bipinnate fashion. Walkom's (1919a) *Stenopteris laxum* (Tenison-Woods) from the Maryborough Basin may also belong to this species. The Indian *Sphenopteris metzgeroides* Harris of Bose and Banerji (1984) and Antarctic *S. nordenskjoldii* Halle, 1913 may be synonymous with *A. bifida* based on frond morphology but both lack fertile material comparable to the Australian species.

Genus *Sphenopteris* (Brongniart) Sternberg, 1825

Type species

Sphenopteris elegans (Brongniart) Sternberg, 1825; Carboniferous; Silesia.

Discussion

Numerous species have been assigned to this cosmopolitan form genus based on subtle differences in pinnule shape and venation pattern. Sphenopterid fronds may represent foliage of true ferns or seed ferns in the absence of fertile material. They are here assigned to the Pteridophyta based on the occurrence of fertile sphenopterid foliage found in coeval strata elsewhere in Australia (Drinnan and Chambers 1986).

Sphenopteris warragulensis McCoy, (in Stirling) 1892

Figure 5C

1993 *Sphenopteris* sp. A; McLoughlin and Guppy; figure 3.

Neotype

NMVP21341 (National Museum of Victoria), Strzelecki Group, Zone C (Barremian–Aptian); Jeetho Valley, Victoria. Designated by Douglas (1973).

Material

WAM P.89.176.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Fragmentary frond at least tripinnate, gross shape uncertain. Rachis reaching 1.5 mm broad with a prominent central longitudinal groove (on mould). First-order pinnae ovate to lanceolate bearing alternately arranged second-order pinnae proximally but giving way to ultimate pinnules distally (Figure 5C). Lanceolate second-order pinnae depart midrib at about 20°. Lanceolate ultimate pinnules arise from second-order pinnae alternately at about 20°, bases decurrent, apices pointed acute, margins entire. Venation sphenopteroid but poorly defined.

Comments

The single Broome Sandstone specimen compares favourably with *Sphenopteris warragulensis* McCoy, (in Stirling) 1892 from Victoria (McCoy in Stirling 1892; Douglas 1973; Drinnan and Chambers 1986) although the details of the fine serrations on pinnules are poorly defined and sori are not preserved. Medwell's (1954a) *Sphenopteris hislopi* Oldham and Morris probably also belongs to *S. warragulensis*. The narrow, elongate, acutely inserted pinnules differentiate this form from most other *Sphenopteris* species. Walkom's (1919a) *S. flabellifolia* Tenison-Woods, 1883 from the Queensland Cretaceous is closely comparable to *S. warragulensis* and would have nomenclatural priority if examination of the Queensland and Victorian specimens established their conspecificity.

South American sphenopterid fronds (Herbst 1964; Baldoni 1980a; Baldoni and de Vera 1980; Petriella and Arrondo 1984) generally differ from *S. warragulensis* by their squat rhomboid or elliptical pinnules. Many Indian Jurassic–Cretaceous sphenopterid species can also be separated from *S. warragulensis* by their more compact elliptical to rhomboid pinnules (Jain 1968; Bose 1958; Bose and Sah 1968). Roy's (1968) *S. specifica* (Feistmantel) appears to have a lesser degree of frond dissection and more elliptical or oblanceolate ultimate pinnules than *S. warragulensis*.

Sphenopteris sp. A

Figures 5G,H

1961 '*Neorhachopteris minuta*' White; p. 303; plate 5, figure 4. [1961a].

cf. 1961 *Ruffordia mortoni* Walkom; White; p. 304; plate 5, figures 6, 7. [1961a].

1993 *Sphenopteris* sp. B; McLoughlin and Guppy; figure 8.

Material

WAM P.64.14, WAM P.89.167, WAM P.89.170, WAM P.89.173, WAM P.89.175 WAM P.89.186.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Frond elliptical, at least bipinnate, 50 mm wide, 85 mm long. Rachis stout (2 mm wide) at base, tapering distally, straight or slightly sinuous. Pinnae arranged alternately at 35°–50° to rachis, linear or arched distally, reaching 4 mm wide, 50 mm long (Figure 5H). Rachilla with prominent central longitudinal ridge (on moulds). Pinnules inserted alternately by contracted or slightly decurrent base. Pinnules rhomboid to elliptical, reaching 2 mm wide, 4 mm long; apices rounded (Figure 5G). Venation dichotomous and gently divergent from base.

Comments

This species is distinguished from *S. warragulensis* by its small elliptical to rhomboid rather than lanceolate pinnules. *Sphenopteris travisi* Stirling and *Sphenopteris* sp. of Drinnan and Chambers (1986) and *Ruffordia mortoni* Walkom, 1928 have more deeply dissected pinnules than *Sphenopteris* sp. A. The Jurassic *Coniopteris* sp. of Hill *et al.* (1966) has similar small rhomboid pinnules but *Sphenopteris* sp. A has much longer and proportionately narrower pinnae.

Herbst's (1964) Argentinian *Sphenopteris* sp. has more rounded pinnules than the Western Australian form but the incomplete specimens of the former inhibit close comparisons. Kasat's (1970) *Cladophlebis* sp. cf. *C. longipennis* Seward from the Indian Early Cretaceous has a very similar gross frond structure to *Sphenopteris* sp. A but its pinnules possess distinct midribs. Other Indian and South African *Sphenopteris* species figured by Jain (1968), Sukh-Dev (1972a), Bose and Sah (1968), and Anderson and Anderson (1985) differ from the Western Australian specimen by their undulate, toothed, or deeply dissected pinnules.

Incertae sedis

Genus *Thinnfeldia* Ettingshausen, 1852**Type species**

Thinnfeldia rhomboidalis Ettingshausen, 1852; Early Jurassic; Steierdorf, Germany.

Thinnfeldia cf. *talbragarensis* Walkom, 1921b

Figures 6A,B

1944 *Thinnfeldia talbragarensis* Walkom; Walkom; p. 203; plate II, figure 8.

1993 *Thinnfeldia* sp.; McLoughlin and Guppy; figure 10.

Material

UWA16690, UWA10472C.

Distribution

Leederville Formation and Bullsbrook Formation (Neocomian–Barremian), Perth Basin.

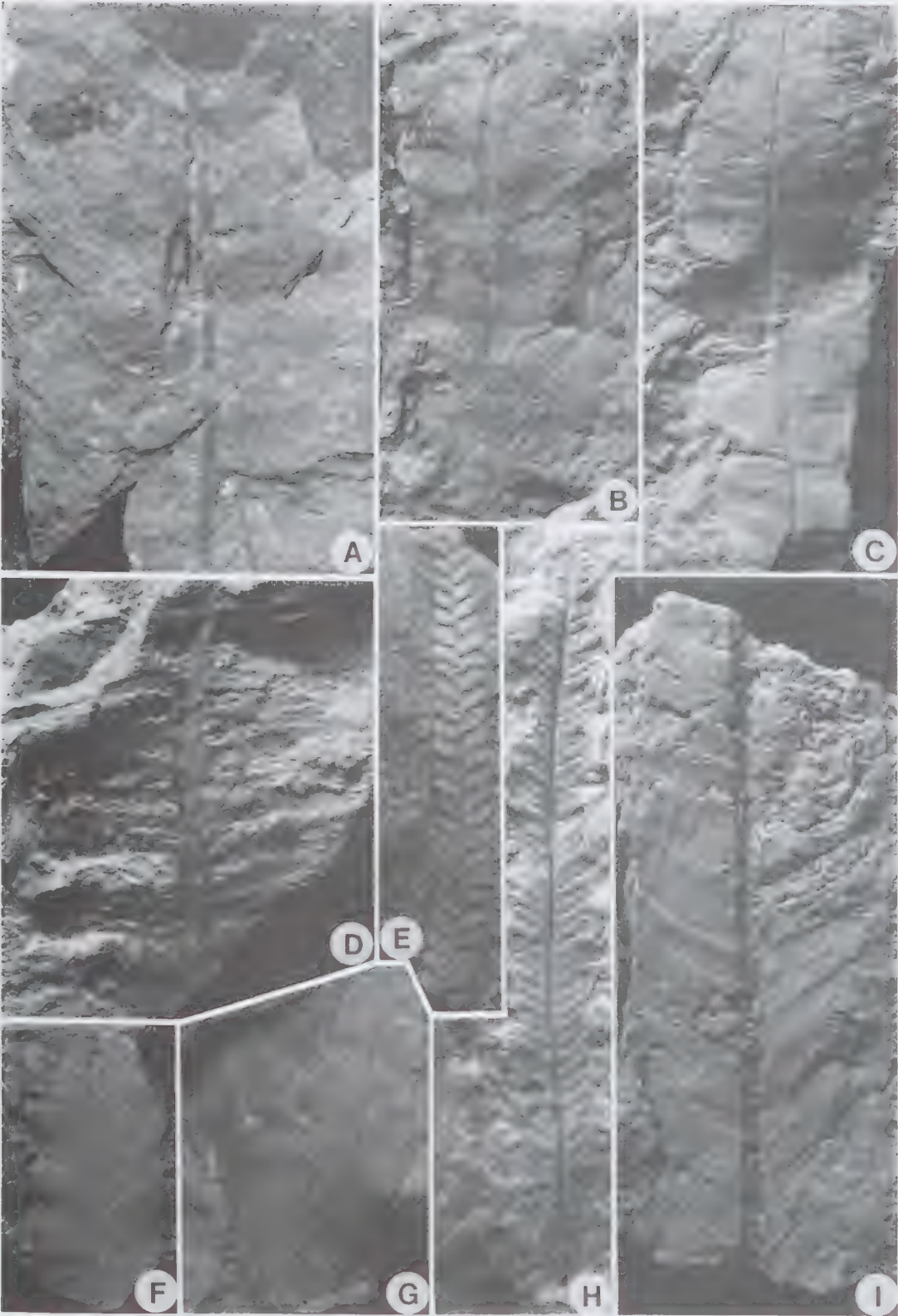
Description

Frond at least bipinnate, >90 mm long, 60 mm wide, elliptical. Rachis robust (<3 mm wide), longitudinally striate. Pinnae opposite, ovate to elliptical, L:W ratio 2:1 to 4:1, arising from rachis at 60°–80°. Pinnae range from undulate-margined to deeply dissected into 4–7 pinnules (Figure 6A). Pinnule arrangement catadromous. Pinnules elliptical, wide-obovate, or rhomboid, reaching 5 mm wide, 8 mm long; subopposite to alternate; apex rounded; base decurrent; venation odontopteroid (Figure 6B).

Comments

Walkom (1944) assigned material from the Leederville Formation to *Thinnfeldia talbragarensis*, a species erected for Jurassic fronds from New South Wales, but these specimens, together with additional specimens from the Bullsbrook Formation, differ from the eastern Australian form in having ovate–elliptical rather than lanceolate pinnules. Walkom's (1944: plate II, figure 8) illustration appears to be upside-down. *Thinnfeldia media* Tenison-Woods, 1883 figured by Jack and Etheridge (1892) from the Burrum Coal Measures, Queensland, and the Victorian *Thinnfeldia* sp. cf. *T. indica* Feistmantel, 1876 of Drinnan and Chambers (1986) which is probably synonymous with *T. maccoyi* Seward, 1904 differ from the Western Australian fronds by their less-dissected lanceolate pinnules.

The Western Australian specimens bear some similarities to *Ruflorinia pilifera* Archangelsky, 1964a from the Cretaceous of Argentina, however, the former specimens lack cuticular details necessary for close comparison to the South



American species. *Thinnfeldia indica* of Zeba-Bano *et al.* (1979) has proportionately more elongate and less dissected leaves than *T. sp. cf. T. talbragarensis*. However, Jain's (1968) ?*Dicroidium* specimen from the Early Cretaceous of eastern India has very similar pinnule shapes and venation to the Western Australian fronds and may be conspecific.

Incertae sedis

Order Pentoxylales

Family Pentoxylaceae

Genus *Taeniopteris* Brongniart 1832

Type species

Taeniopteris vittata Brongniart, 1832; Jurassic; Whitby, England.

Taeniopteris daintreei McCoy, 1874

Figures 6C,F,G; 7A

1944 *Taeniopteris spatulata* McClelland; Walkom; p. 203; plate II, figure 9.

1961 *Taeniopteris cf. T. elongata* Walkom; White; p. 303; plate figures 1B, 2B. [1961a].

1993 *Taeniopteris daintreei*; McLoughlin and Guppy; figure 14; figure 18.

Lectotype

NMVP12270 (National Museum of Victoria); Strzelecki Group, Zone C (Valanginian–Albian); Cape Paterson, Victoria. Selected by Drinnan and Chambers (1985).

Material

WAM P.64.12, WAM P.64.15, WAM P.74.26, WAM P.74.27, WAM P.74.28, WAM P.74.29, WAM P.74.32, WAM P.74.33, WAM P.74.34, WAM P.88.8, UWA16685, UWA16682, UWA16683, UWA10374A,B,E, UWA10375, UWA10376, UWA-10461A,B,C, UWA10463, UWA10464B,F,G,J,K, UWA10466A, UWA10470C,D, UWA10472B, UWA10474A, UWA10477A,C.

Distribution

Widespread; probably upper Lower Jurassic to Lower Cretaceous of Australasia. Western Australia: Broome Sandstone, Canning Basin; Cronin Sandstone, Officer Basin; Bullsbrook and Leederville Formations, Perth Basin.

Description

Leaves simple, up to 2 cm wide and 8.3 cm long, lorate, linear, or spatulate. Margin entire or gently undulate, apex rounded obtuse, base tapering acute, petiolate. Midrib longitudinally striate, robust (up to 2 mm wide), gently tapering distally, persistent. Secondary veins closely spaced, depart midrib at $>60^\circ$, bifurcate once or twice then pass straight to margin at 75° – 90° . Lamina rarely shows undulate folds. Attached fertile organs and cuticle unavailable.

Comments

Drinnan and Chambers (1985) provided a detailed account of this Early Cretaceous species based on material from Victoria. They suggested a relationship between *T. daintreei* leaves and both the pollenate fructification *Sahnia laxiphora* Drinnan and Chambers, 1985 and the ovulate pentoxylean fructification *Carnoconites cranwellii* Harris, 1962, based on their co-occurrence in the Koonwarra fossil bed of the Gippsland Basin and similar co-fossilized forms in New Zealand, New South Wales and India (Blaschke and Grant-Mackie 1976; White 1981; Visshnu-Mittre 1953; Rao 1981). Drinnan and Chambers (1985) provisionally excluded White's (1981) New South Wales Jurassic *Taeniopteris spatulata* McClelland, 1850 from *T. daintreei* due to the discrepancy in the ages of the Victorian and New South Wales specimens. Differences in the preservation of associated fruiting bodies also inhibited close comparison. However, Drinnan and Chambers (1985) noted that previous distinctions between Victorian Cretaceous *T. daintreei* and Indian Jurassic–Cretaceous *T. spatulata* cuticle morphologies are probably less significant than initially suggested (Rao 1943; Douglas 1969; Visshnu-Mittre 1957). The Western Australian specimens are morphologically indistinguishable from Victorian *T. daintreei* leaves.

Taeniopteris daintreei-like leaves are common components of several other Middle Jurassic to Early Cretaceous floras within Australia and New Zealand (Dun 1898; Walkom 1919b, 1944; Glaessner and Rao 1955; White 1961a, b; Gould 1980; Blaschke and Grant-Mackie 1976). Several authors (e.g., Chapman 1909; Glaessner and Rao 1955; Douglas 1969; Baldoni and de Vera 1980; Drinnan and Chambers 1985) have figured or described leaves which show varying degrees of lamina dissection, in some cases making them gradational with forms attributable to *Nilssonina*

- ◀ **Figure 6** A,B, *Thinnfeldia cf. talbragarensis* Walkom, 1921; (A) UWA16690, Portion of frond, Leederville Formation, $\times 1$; (B) UWA10472C, Isolated pinna, Bullsbrook Formation; $\times 4$; C,F,G, Portions of variably dissected *Taeniopteris daintreei* McCoy, 1874 leaves; (C) UWA24640B, Bullsbrook Formation, $\times 1.5$; (F) UWA120484, Broome Sandstone, $\times 3$; (G) WAM P.74.26a, Bullsbrook Formation, $\times 1.5$; D,E,H,I, *Ptilophyllum cutchense* Morris (in Grant) emend. Bose and Kasat, 1972; (E) WAM P.88.7, Broome Sandstone, $\times 2$; (H) WAM P.88.4, Broome Sandstone, $\times 0.9$; (I) UWA118836, Bullsbrook Formation, $\times 3$.

Brongniart 1825. Several specimens from the Bullsbrook Formation also display variable dissection but differ from *Nilssonsonia* species herein which show distinct gaps between lamina segments (pinnules).

Incertae sedis

Pinnate frond

Figure 6D

Material

UWA10475.

Distribution

Bullsbrook Formation (Neocomian–Barremian), Perth Basin, Western Australia.

Description

A single poorly preserved pinnate frond of uncertain affinities occurs in the Bullsbrook Formation assemblage. Frond 4 cm long, 2.2 cm wide, base and apex absent. Rachis broad (3 mm), longitudinally striate, gently tapering distally; pinnules linear with full basal attachment, margins entire or gently undulate, venation indistinct (Figure 6D).

Remarks

This specimen may represent a fern, seed-fern, or cycadophyte frond. The apparently undulate margins on some pinnules invite comparison to Douglas's (1969) *Pachypteris austropapillosa* recorded from coeval "Zone B" floras of the Victorian Early Cretaceous but the specimen is too poorly preserved for identification.

Division Cycadophyta

Order Bennettitales

Genus *Nilssonsonia* Brongniart, 1825

Type species

Nilssonsonia brevis Brongniart, 1825; Rhaetian; Hoer, Sweden.

Nilssonsonia sp. A

Figure 7F

1993 *Nilssonsonia* sp. A; McLoughlin and Guppy; p. 14; figure 15.

Material

WAM P.96.3.

Distribution

Nanutarra Formation (Neocomian–?Aptian), Carnarvon Basin.

Description

Fragmentary pinnate fronds with broad striate rachis (<5 mm wide). Pinnules subopposite, truncate elliptical, semicircular, oblong, or slightly falcate, up to 15 mm wide and 25 mm long; apex rounded, asymmetrical; full basal attachment; inserted laterally? or adaxially? on rachis (Figure 7F). Pinnule bases expanded slightly, basiscopic margin rounded convex, acroscopic margin straight or slightly concave. Generally >10 veins arising from pinnule base, each bifurcates no more than twice (rarely more than once), passing subparallel to apical and lateral margins without anastomoses.

Comments

The full basal insertion of pinnules on the rachis distinguishes this leaf-form from *Otozamites* species which have pinnules with contracted bases (Taylor and Taylor 1993). White's (1961b) *Pterophyllum fissum* Feistmantel leaves are pinnatifid in contrast to the pinnate *Nilssonsonia* sp. A. Several *Nilssonsonia* and *Ctenozamites* species from the Yorkshire Jurassic (Harris 1964) have similar sized fronds to the Western Australian examples but differ in the details of their pinnule shapes and venation.

Nilssonsonia sp. B

Figure 7B

1993 *Nilssonsonia* sp. B; McLoughlin and Guppy; p. 14; figure 17.

Material

WAM P.88.5, WAM P.88.6.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Fragmentary elliptical to oblanceolate pinnate fronds, petiolate; rachis up to 2 mm wide. Pinnules with full basal attachment, semicircular to oblong, apex rounded. Basiscopic margin of pinnules gently convex, acroscopic margin straight or slightly concave (Figure 7B). Pinnules alternate, up to 12 mm wide, 22 mm long. Numerous closely spaced, fine, indistinct, veins emerge from rachis, diverge gently towards apex and lateral margins; bifurcations rare, anastomoses absent.

Comments

This leaf form differs from *Nilssonsonia* sp. A by its more divergent and closely spaced venation. White's (1961a) and Walkom's (1919a) *Nilssonsonia schaumbergensis* Dunker from the Broome Sandstone and Burrum Coal Measures respectively

both have broader and shorter lamina segments than either of the Western Australian *Nilssonia* species described here. White's (1981) *Nilssonia compta* (Phillips) Brongniart also has substantially shorter wedge-shaped pinnules. By contrast, *Nilssonia plutovillensis* Walkom, 1928 has narrower pinnules with more acute apices.

Genus *Ptilophyllum* Morris emend. Bose and Kasat, 1972

Type species

Ptilophyllum acutifolium Morris, (in Grant) 1840; Early Cretaceous; south of Charivar Range, India.

Discussion

Otozamites Braun, in Münster 1843 is traditionally distinguished from *Ptilophyllum* by the asymmetrical, expanded (auriculate) bases of its pinnules (Seward 1917). However, the genera may be synonymous as several *Ptilophyllum* species also possess asymmetrical auriculate pinnules (Bose and Kasat 1972). In the absence of cuticular data, Western Australian bennettitalean fronds with narrow pinnules can be compared with a wide range of *Otozamites* and *Ptilophyllum* species (Bose and Kasat 1972; Bose 1974).

***Ptilophyllum acutifolium* Morris, (in Grant) 1840
Figures 7I,J**

1961 *Zamites* sp.; White; p. 305; plate 8, figure 3. [1961a].

1993 *Ptilophyllum acutifolium*; McLoughlin and Guppy; p. 14; figure 16.

Lectotype

V21330, British Museum (Natural History); Jabalpur Series equivalents (Lower Cretaceous); Kutch, India. Selected by Bose and Kasat (1972).

Material

WAM P.64.16, WAM P.89.162 WAM P.96.2, WAM P.96.4.

Distribution

Lower Cretaceous of India; possibly Jurassic and Lower Cretaceous of South America; Nanutarra Formation, Carnarvon Basin; Broome Sandstone, Canning Basin (both Lower Cretaceous), Western Australia.

Description

Fragmentary, broadly elliptical pinnate fronds. Rachis stout (1–2.5 mm wide). Pinnules subopposite to alternate, linear, straight or arched distally, inserted on adaxial surface of rachis at

30°–65°, up to 3 mm wide, 40 mm long (Figures 7I,J). Pinnule bases rounded, apices pointed acute or truncate. Pinnules aligned in a common plane or slightly imbricate. Several veins enter base of pinnules, diverge slightly, pass straight to apical margin, no anastomoses.

Comments

Ptilophyllum acutifolium is distinguished from other bennettitalean fronds in the collection by its very narrow and elongate pinnules which may be straight or gently falcate. This species is common within the Broome Sandstone and Nanutarra Formation and was identified by White (1961a) as *Zamites* sp. *Ptilophyllum acutifolium* is widely recorded from the Indian Early Cretaceous (Morris in Grant 1840; Feistmantel 1877a, b, c, 1879; Sahni and Rao 1933; Bose and Kasat 1972; Sukh-Dev and Zeba-Bano 1980; Baksi and Naskar 1981; Bose and Banerji 1984). South American Jurassic and Early Cretaceous fronds have also been assigned to this species (Arrondo and Petriella 1980; Longobucco *et al.* 1985) although both the Australian and South American forms tend to have longer pinnules than the Indian examples.

***Ptilophyllum cutchense* Morris, (in Grant)
emend. Bose and Kasat 1972
Figures 6E,H,I; 7C,D**

1944 *Ptilophyllum pecten* (Phillips); Walkom; p. 204; plate II, figure 6.

1961 *Ptilophyllum pecten* (Phillips); White; p. 302–305; plate 6, figure 3D; plate 8, figure 1. [1961a].

1961 *Otozamites bengalensis* Oldham and Morris; White; p. 305; plate 7, figure 5. [1961a].

1993 *Otozamites bengalensis*; McLoughlin and Guppy; p. 14; figures 13, 14.

Lectotype

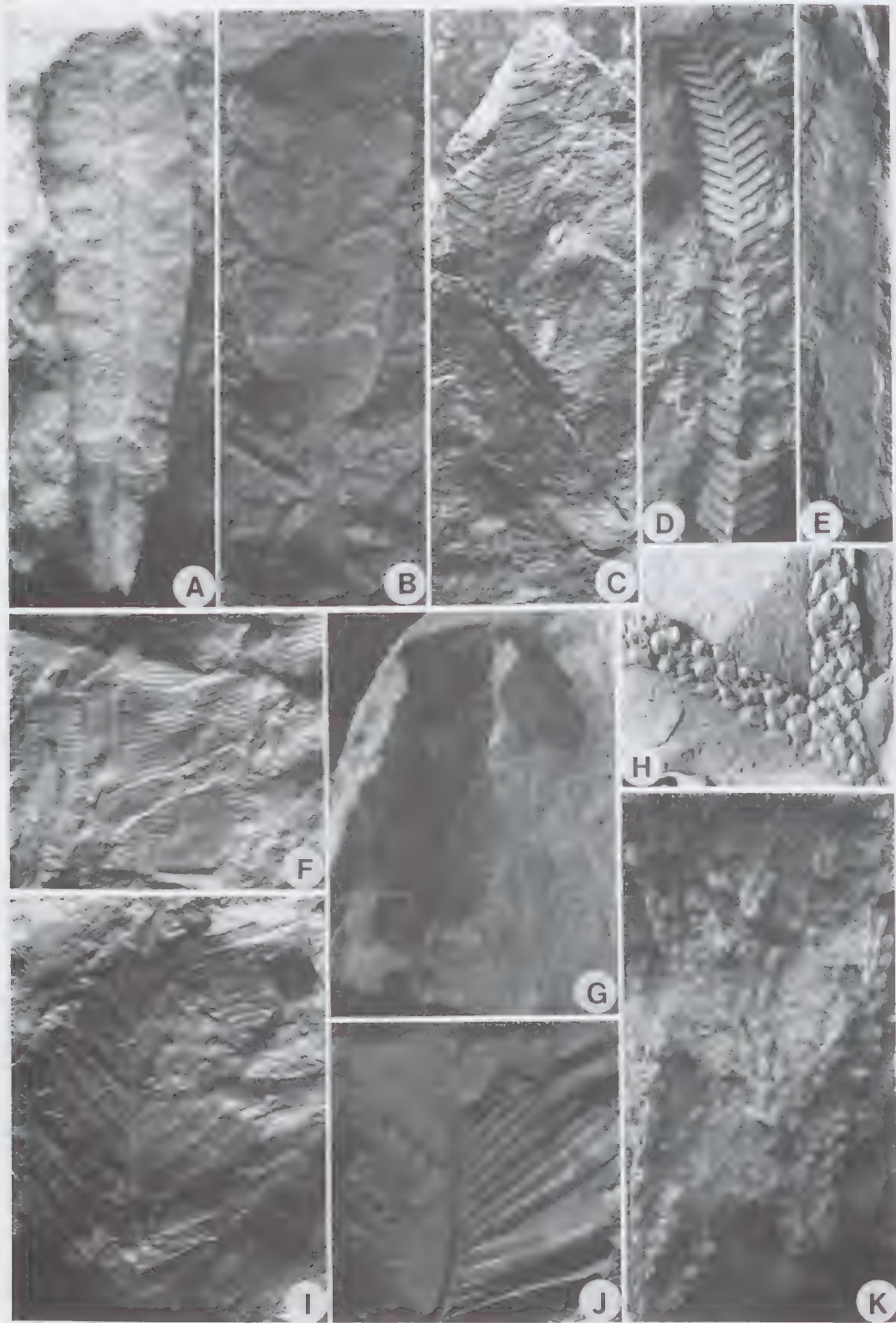
V20191 (9943), British Museum (Natural History); Rajmahal Series equivalents (?Lower Cretaceous); Kutch, India. Selected by Bose and Kasat (1972).

Material

WAM P.64.6, WAM P.64.7, WAM P.64.8, WAM P.64.13, WAM P.70.46, WAM P.86.57, WAM P.86.172, WAM P.88.4, WAM P.88.7, WAM P.88.11, WAM P.89.169, UWA16684, UWA118836.

Distribution

Broome Sandstone, Canning Basin; Leederville and Bullsbrook Formations, Perth Basin (all Neocomian–Barremian).



Description

Fronds linear, pinnate, petiolate, up to 16 mm wide, 155 mm long. Rachis stout, up to 1 mm thick. Pinnules inserted adaxially on rachis. Pinnule base slightly auriculate or contracted (Figure 7C). Adjacent pinnules slightly imbricate. Pinnule bases abutting alternately on adaxial surface of rachis forming a zig-zag pattern on impressions (Figures 6E, 7D). Pinnules oblong or falcate, apices pointed acute, slightly inclined distally (Figures 6H,I). Pinnules arise at 50°–70° from rachis, reaching 8 x 2 mm. Veins emerge from centre of pinnule base, dichotomize, slightly diverge, intersect apical and lateral margins without anastomoses.

Comments

In gross morphology these fronds are similar to a number of bennettitalean foliage species including *Ptilophyllum pecten* (Phillips) Harris, 1969, *P. horridum* Roy, 1963, *P. canthifera* Douglas, 1969, and *Otozamites exhislopi* Bose, 1974. However, the contracted pinnule bases, slightly expanded basiscopic pinnule lamina, pinnule imbrication, and relatively short, slightly falcate pinnules with obtuse apices suggests that the Western Australian specimens are better assigned to *P. cutchense* Bose and Kasat, 1972, a common Jurassic? to Early Cretaceous species of India and Australia (Walkom 1944; Glaessner and Rao 1955; White 1961a,b; Bose and Kasat 1972). Most previous Australian studies have assigned such remains to *Otozamites bengalensis* (Oldham and Morris) Schimper, 1870 but Bose and Kasat (1972) transferred the type specimens of that species to *P. cutchense*. Walkom's (1917a, 1919a) *Ptilophyllum pecten* specimens from the Lower Cretaceous Stanwell and Burrum Coal Measures may also belong to *P. cutchense* based on pinnule morphology.

Several *Otozamites* species identified by Walkom (1921b) from the Yarragadee Formation, northern Perth Basin, have much broader and either substantially longer or shorter pinnules than *P. cutchense* and are probably of Middle to Late Jurassic age based on palynological studies of that unit (Backhouse 1988).

Ptilophyllum boolensis (Douglas) Douglas, 1969 Figure 7G

1993 *Ptilophyllum boolensis*; McLoughlin and Guppy; p. 14; figure 21.

Holotype

GSV58781 (Geological Survey of Victoria); Strzelecki Group, Zone B (Neocomian); Boola Boola Forest, Gippsland, Victoria (Douglas 1969).

Material

WAM P.96.13.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin; Strzelecki Group, Zone B (Neocomian), Victoria.

Description

Single diminutive lanceolate pinnate frond fragment preserved as an impression in siliceous siltstone. Rachis slender (<1 mm wide). Pinnules attached to upper surface of rachis. Pinnules very small (<3 mm wide, <5 mm long), circular to elliptical, bases truncate to auriculate, apices broadly rounded (Figure 7G). Pinnules inserted alternately at about 50° to rachis; adjacent pinnules slightly overlap producing a zig-zag pattern along rachis. Single vein enters centre of pinnule base and dichotomizes two or three times, ultimate veins diverging straight to lateral and apical margins.

Comments

Although Douglas' (1969) *Ptilophyllum boolensis* specimens were defined partly on cuticular features not available for the Western Australian specimens, the Broome Sandstone frond (Figure 7G) appears to be attributable to this species based on its size and circular to elliptical pinnules. *Otozamites pecten* Sitholey, 1984 from the ?Jurassic of India is a similar diminutive frond with rounded, partly overlapping, pinnules. Furthermore, its squat, sinuous-walled, papillate

◀ **Figure 7** **A**, *Taeniopteris daintreei* McCoy, 1874; WAM P.64.15; Broome Sandstone; x 2; **B**, *Nilssonsonia* sp. B; Base of frond; WAM P.88.5; Broome Sandstone; x 2; **C,D**, *Ptilophyllum cutchense* Morris (in Grant) emend. Bose and Kasat, 1972; (C) UWA16684, Leederville Formation, x 1.5; (D) WAM P.88.172; Broome Sandstone; x 1; **E**, *Zamia* sp.; isolated pinnule; UWA118826; Bullsbrook Formation; x 2; **F**, *Nilssonsonia* sp. A; fragmentary pinnules; WAM P.96.3; Nanutarra Formation; x 1.5; **G**, *Ptilophyllum boolensis* (Douglas) Douglas, 1969; WAM P.96.13; Broome Sandstone; x 6; **H**, *Araucaria* sp. B; WAM P.90.1; latex cast of axis with imbricate leaves; Broome Sandstone; x 5; **I,J**, *Ptilophyllum acutifolium* Morris (in Grant), 1840; (I) WAM P.96.2, apical portion of frond, Nanutarra Formation, x 2; (J) WAM P.89.162, Broome Sandstone, x 1; **K**, silicon cast of *Araucaria* sp. A; slender branches with elongate rhomboid leaves; WAM P.96.7; Broome Sandstone; x 3.

epidermal cells are closely comparable to the epidermal/cuticular morphology of *P. boolensis* suggesting a close relationship. *Ptilophyllum boolensis* is restricted to Douglas' (1969) "Zone B" flora in Victoria and its occurrence within the Broome Sandstone suggests that this unit is, at least partly, also of Neocomian age.

Genus *Zamites* Brongniart, 1828

Type species

Zamites gigas (Lindley and Hutton) Morris, 1843; Jurassic, Scarborough, England. Selected by Andrews (1970).

Zamites sp.

Figure 7E

Material

UWA118826.

Distribution

Bullsbrook Formation, Perth Basin (Neocomian–Barremian).

Description

Linear pinnule 46 mm long, 5 mm wide, base contracted, apex rounded obtuse, margin entire (Figure 7E). Several veins emerge from base, rarely dichotomize immediately above base producing 10 ultimate veins which pass parallel along the lamina and slightly converge near apex. Complete frond and cuticular data not available.

Comments

The single available pinnule is similar to the linear parallel-veined leaflets of *Zamites* or *Pseudoctenis* fronds from the Early Cretaceous of South Africa (Anderson and Anderson 1985) and India (Sahni and Rao 1933) but specific identification is not possible without complete fronds or cuticular data.

Division Pinophyta

Class Pinopsida

Order Pinales

Family Araucariaceae

Genus *Araucaria* Jussieu 1789

Type species

Araucaria araucana (Molina) K. Koch, 1873; extant; Chile.

Discussion

Three species of *Araucaria* are recognized from

the Western Australian Cretaceous on the basis of leaf size and shape and axis thickness. These species may represent different portions or stages of maturity of the same plant. Until intermediate or more complete remains are found the foliage types are described separately.

Araucaria sp. A

Figure 7K

1993 *Araucaria* sp. A; McLoughlin and Guppy; figure 22.

Material

WAM P.63.31, WAM P.96.7.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Slender terminal axes <4 mm wide, reaching 36 mm long, bearing spirally inserted simple scale-like leaves closely adpressed to axis (Figure 7K). Branches rare, irregular. Leaves small (1 mm wide, 2 mm long), elliptical, ovate, or rhomboid, with prominent ridge along midline of abaxial surface (on casts). Leaves tightly imbricate; overlapping by about one-third those in distally adjacent spiral. Leaf apices acutely pointed, commonly flexed adaxially.

Comments

Araucaria sp. A differs from other Western Australian araucarians by its very small, longitudinally elongate, rhomboid leaves that typically show a ridge along the centre of the abaxial leaf surface casts. In this respect the leaves are very similar to *Brachyphyllum* sp. of Banerji and Pal (1986) from the Upper Jurassic Sarnu Hill Formation, India. Araucarioid axes from the Yaragadee Formation (Middle to Late Jurassic), Perth Basin, described as *Pagiophyllum* or *Brachyphyllum* species or coniferous fragments by Arber (1910), Walkom (1921b), and White (1986) have narrower leaves that are not adpressed to the axis and belong to a separate araucarian species.

A number of other Australian and South American forms, including *Brachyphyllum gippslandicum* McCoy (in Stirling), 1892, *Araucaria* sp. of Drinnan and Chambers (1986), *Brachyphyllum* sp. of Baldoni (1980a), and *Nothopheuen brevis* Del Fueyo, 1991, are morphologically similar to *Araucaria* sp. A but their precise relationships will only be resolved when cuticular data and fructifications become available.

Araucaria sp. B

Figures 7H; 8A–C,F

1993 *Araucaria* sp. B; McLoughlin and Guppy; figure 26.

Material

WAM P.89.188, WAM P.89.189, WAM P.89.190, WAM P.90.1, WAM P.90.3, WAM P.96.14.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Axes slender to robust (2–9 mm wide, reaching at least 70 mm long) bearing spirally arranged, broadly rhomboid, scale-like leaves (Figures 7H, 8F). Axes linear or variably curved, giving off lateral branches at irregular intervals (Figures 8B,C). Leaves squat, remaining attached and adnate to axis, basally contiguous forming a rhomboid, pentagonal or hexagonal pattern on axis impressions (Figures 8A,C). Leaves attached to axis by broad base, apex contracted to a short (<0.5 mm) spine. Variations in the average basal width of leaves occurs along some axes reflecting seasonal growth. Leaves most often apically compressed, apparently fleshy or leathery in original state, venation indistinct. When laterally compressed, leaves slightly overlap bases of those in succeeding spiral.

Comments

Numerous Australian Mesozoic axes bearing rhomboid leaves, and often assigned to *Brachyphyllum* or *Allocladus* species (e.g., Seward 1904; Chapman 1904; Walkom 1917b, 1919a, 1921a, 1928; Medwell 1954a; Hill *et al.* 1966; Townrow 1967; White 1961a, 1981), may belong to the Araucariaceae, Podocarpaceae, Taxodiaceae, Cupressaceae, or Cheirolepidaceae. In this instance, association with araucarian cone scales favours an araucarian affinity, however, further morphological details and attached fertile material will be needed to clearly establish the affinities of *Araucaria* sp. B.

Brachyphyllum rhombicum Feistmantel of Sahni (1928) is closely comparable to *Araucaria* sp. B whereas his *B. mamillare* Brongniart has more elongate rhomboid leaves. The Early Cretaceous Indian *Brachyphyllum bansaensis* and *B. eikaiostomum* of Sukh-Dev and Bose (1974) are differentiated on epidermal/cuticular details but are otherwise difficult to distinguish from *Araucaria* sp. B. Baksi's (1968) *Brachyphyllum rhombicum* (Lindley and Hutton) Sahni is also very similar but its leaves are more axially elongate. The South African *Araucaria rogersii* (Seward) Anderson and Anderson, 1985 has

spirally arranged rhomboid leaves similar to those of *Araucaria* sp. B. However, closer comparison is not possible owing to the lack of cuticular details or pollenate cones associated with the Western Australian material.

Araucaria sp. C

Figure 8E

Material

WAM P.88.16.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Robust bifurcate axis clothed in spirally arranged?, flattened, lanceolate or linear leaves (Figure 8E). Length from base to bifurcation 14 cm, terminal branches both 8 cm long. Maximum width of axis 20 mm. Leaves reaching 4 mm wide, 30 mm long, smooth or with indistinct longitudinal striae, possibly contracted slightly at base, apices pointed acute. Detached leaf imprints on same slab reach 5 mm wide, 60 mm long.

Comments

The available specimen is too poorly preserved for close comparison to other illustrated material. It probably represents an araucarian conifer branch bearing dense, flattened, spirally arranged, lanceolate to linear leaves similar to the modern Australian Bunya Pine (*Araucaria bidwilli* Hooker, 1843). The leaves and branched axis of *Araucaria* sp. C are much more robust than the other species of *Araucaria* described from the Broome Sandstone.

Araucarian cones

Figure 8D

Material

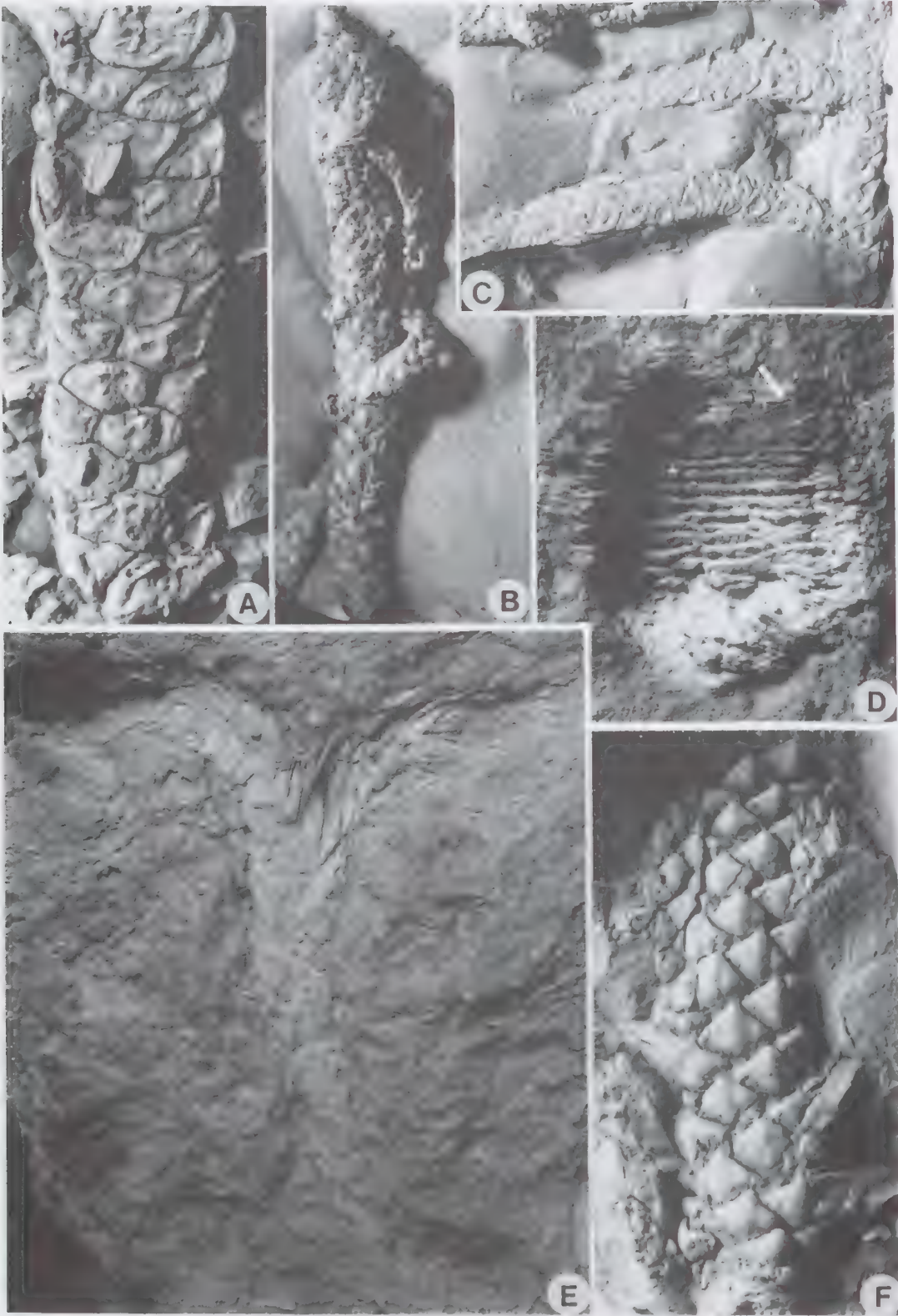
WAM P.89.185, WAM P.89.187.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Two cone impressions available, both c. 5 x 4 cm, longitudinally elliptical in outline (Figure 8D). Cones feature >15 transverse ridges (on casts) marking positions of closely spaced cone scale spirals (ridges 1.5 mm apart). Individual cone scales poorly differentiated, apices extended as 6 mm long flanges or spines that arch distally at



periphery of cone. Cone attachment point not evident. Seeds and foliage not available.

Comments

Both of the Broome Sandstone cones are isolated and can not be linked to any of the araucarian foliage species described above. Latex casts failed to reveal significant morphological details of cone scale shapes although their large size suggests that the cones are ovulate rather than pollenate. Anatomical details are not preserved in the Western Australian specimens preventing comparison to permineralized araucarian cones from the Jurassic? of India (Bohra and Sharma 1980). An araucarian cone from the Kennedy Ranges (Merlinleigh Sandstone: Eocene), Western Australia, figured by McLoughlin and Hill (in press) is of similar dimensions but has more distinctive cone scale impressions which in some cases have left prominent spirally arranged rhomboid scars on the cone axis.

Araucarian cone scales

Figures 9A,B

1993 Araucarian cone scale; McLoughlin and Guppy; figure 20.

Material

WAM P.96.5, WAM P.96.6.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Detached cone scale complex (fused ovuliferous scale, seed, and bract). Scale cuneate, base pointed acute to truncate, apex truncate, no terminal spine evident (though possibly removed); width 13 mm, length 12–14 mm. Scales with elliptical to oblong indentation or cast (2.5 mm wide, 8 mm long) near base marking position of seed (Figures 9A,B). Cone scale narrowly winged.

Comments

Two cone scales are preserved in the Broome Sandstone assemblages. Similar isolated cone scales are found throughout Gondwanan Jurassic and Cretaceous strata but their affinities with foliage-based species are generally indeterminate. The Broome specimens lack apical spines in contrast to

most South American and eastern Australian cone scales (Walkom 1919a; Baldoni 1981; Drinnan and Chambers 1986). They also appear to have poorly developed lateral membranous wings although this may be a preservational flaw. The Broome cone scales are most similar to *Araucarites* sp. B of Seward (1904) and the “winged seed type 1” of Drinnan and Chambers (1986). Indian Mesozoic cone scales assigned to *Araucarites parsorensis* Lele, 1955 and Baksi’s (1968) *A. cutchensis* Feistmantel are not as apically expanded as the Western Australian specimens. *Araucarites janaianus* Bose and Banerji, 1984 is similar in size and ovule position to the Western Australian scales but it possesses distinct apical spines.

Family Podocarpaceae

Genus *Elatocladus* Halle emend Harris, 1979

Type species

Elatocladus heterophylla Halle 1913; ?Lower Jurassic or ?Lower Cretaceous; Hope Bay, Antarctic Peninsula.

Elatocladus ginginensis sp. nov.

Figures 9C–E,G

1961 *Elatocladus plana* (Feistmantel); White; p. 302–303; plate 6, figures 1A, 2A. [1961a].

1993 *Rissikia* sp.; McLoughlin and Guppy; p. 14; figure 24.

Holotype

UWA16703; Leederville Formation (Neocomian–Barremian); Cheriton Creek, Gingin, Western Australia.

Material

WAM P.88.14, WAM P.89.174, WAM P.89.192, WAM P.96.10, UWA10464C–E, UWA10466B–E, UWA10467A,B, UWA10468A, UWA10474B, UWA10475, UWA10477B, UWA16703.

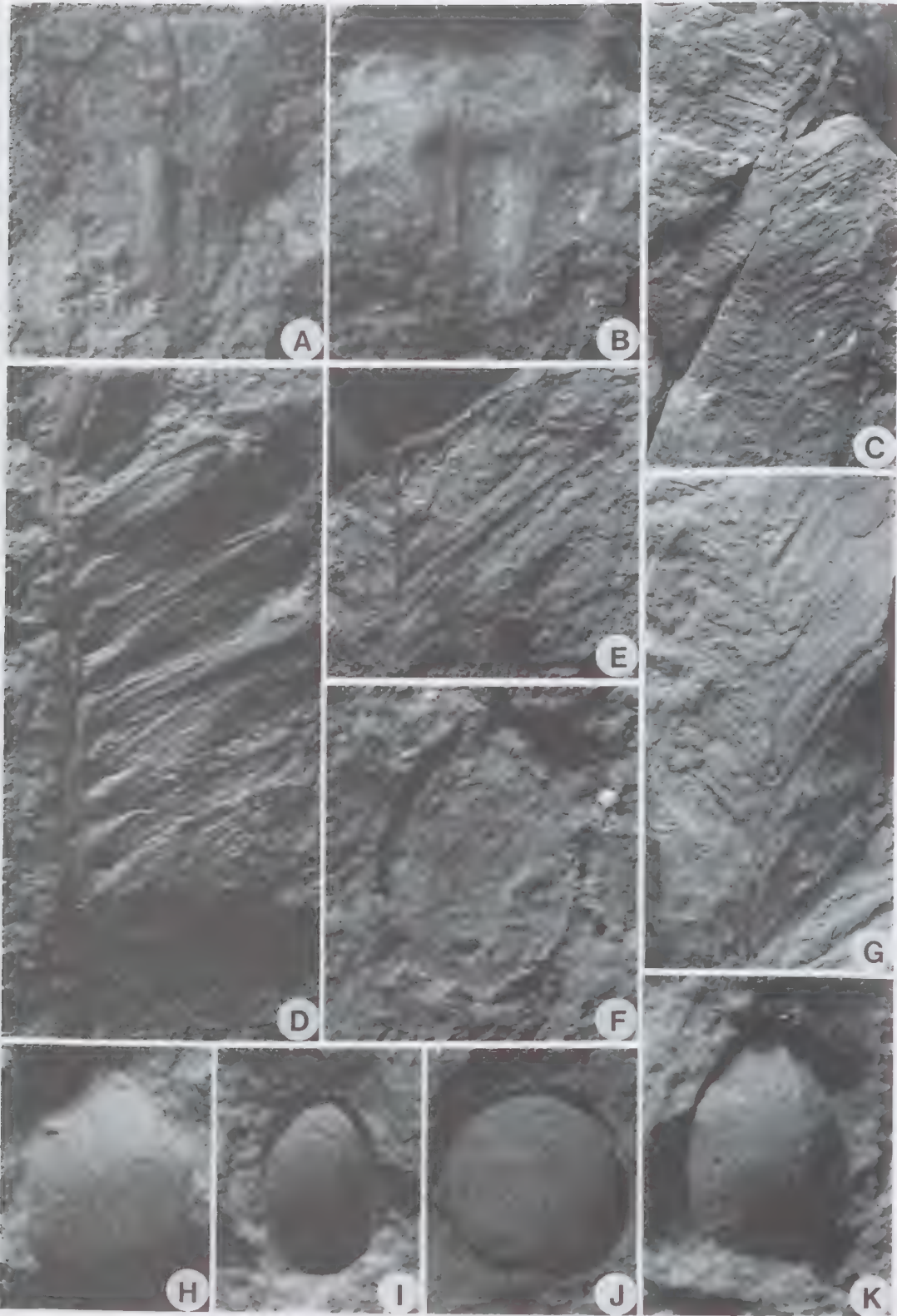
Distribution

Broome Sandstone, Canning Basin; Leederville and Bullsbrook Formations, Perth Basin (all Neocomian–Barremian).

Diagnosis

Slender distal shoots bearing univeined, spirally inserted, basally twisted, linear leaves in distichous

◀ **Figure 8** A–C, F, *Araucaria* sp. B; latex casts of branches bearing spirally arranged rhomboid leaves; (A) WAM P.89.188, x 4; (B) WAM P.89.189, x 3; (C) WAM P.89.189, x 2; (F) WAM P.89.188, x 6; all from Broome Sandstone; D, Araucarian cone impression; distal end at top of figure; WAM P.89.187; Broome Sandstone; x 15; E, *Araucaria* sp. C; large branched axis impression with overlapping scale-like leaves; WAM P.88.16; Broome Sandstone; x 0.8.



arrangement. Leaves flattened; apices bluntly rounded; bases slightly contracted to slightly decurrent.

Description

Slender terminal axes (reaching 3 mm wide and 51 mm long) bearing numerous univeined linear leaves (Figures 9C,E,G). Leaves spirally inserted although basally twisted to lie in a common plane. Leaves inserted on branches at 40°–90°. Leaves up to 1 mm wide, 20 mm long, flattened, straight or slightly flexed distally, apices rounded. Leaf bases slightly contracted but not significantly petiolate, slightly decurrent (Figure 9D).

Comments

Harris 1979 emended *Elatocladus* Halle, 1913 to exclude the morphology of the leaf bases as a diagnostic character thus incorporating specimens previously assigned to both *Elatocladus* and *Rissikia* Townrow, 1967. It should be noted, however, that some workers (e.g., Anderson and Anderson, 1989) have maintained a distinction between these genera based on the presence of contracted leaf bases in *Elatocladus* and decurrent leaf bases in *Rissikia*. In the absence of attached reproductive organs the Western Australian material is insufficiently abundant or well preserved to resolve this taxonomic issue and the specimens are assigned to a new species within Harris' (1979) broader definition of *Elatocladus*. Numerous species from the Gondwanan Mesozoic attributed to *Elatocladus*, *Rissikia*, or other podocarpacean genera have often been distinguished by slight differences in leaflet size, shape, leaf arrangement, and petiole characters (Petriella and Arrondo 1984).

Elatocladus ginginensis sp. nov. lacks cuticle but is distinguished from other species by the size of its slender leaves, rounded leaf apices, and decurrent lamina bases which are not as significantly contracted as those of *Elatocladus longifolium* Baldoni, 1980b, *E. plana* (Feistmantel) Seward 1919, or *Morenoa fertilis* Del Fueyo, Archangelsky, and Taylor 1990. White's (1961a) *Elatocladus plana* specimens from the Cronin Sandstone have identical leaflet characters and are reassigned to *E. ginginensis*. The *E. plana* specimens of Glaessner and Rao (1955) from the Early Cretaceous of South Australia are described as having leaves with full basal attachment, a feature not consistent with *Elatocladus*. Their specimens may be synonymous with *E. ginginensis* although their illustrations do

not allow close comparison. Other Australian specimens assigned to *E. plana* (Hill *et al.* 1966; Walkom 1919a); and *Rissikia talbragarensis* White, 1981 have either substantially longer or broader leaves which show a dense but regular spacing not evident in *E. ginginensis*.

Elatocladus conferta (Oldham and Morris) Sahnii, 1928 and *E. kingianus* Bose, Kutty, and Maheshwari, 1982 specimens of Halle (1913), Sah (1965), Maheshwari and Singh (1976), Bose and Banerji (1984), and Walkom (1928) have substantially smaller leaves than *E. ginginensis*. Permineralized remains assigned to *E. sahnii* Vishnu-Mittre, 1957 from the Indian Jurassic have similar decurrent bases but the absence of anatomical details in the Western Australian specimens prevents closer comparison. Extra-Gondwanan *Elatocladus* species are more readily distinguishable on gross leaf morphology or cuticular details (e.g., Miller and Lapaska 1985; Kimura and Ohana 1988, 1989; Kimura *et al.* 1991).

Incertae sedis

Genus *Carpolithes* Brongniart 1822

Type species

Carpolithes thalictroides Brongniart, 1822; Tertiary; France and England.

Carpolithes bullsbrookensis sp. nov.

Figures 9F,H–K

1993 *Carpolithes* sp. McLoughlin and Guppy; figure 19.

Holotype

UWA10469A; Bullsbrook Formation (Neocomian–Barremian); 2.5 km northeast of Bullsbrook Hotel, Perth Basin.

Material

UWA10374C,D, UWA10462B, UWA10464H,I, UWA10468B, UWA10469A,B–F, UWA10473A.

Distribution

Bullsbrook Formation (Neocomian–Barremian); Perth Basin.

Diagnosis

Ovate to elliptical wingless seeds, reaching 5 x 7

◀ Figure 9 A,B, Araucarian cone scales; (A) WAM P.96.5; (B) WAM P.96.6; Broome Sandstone; both x 4; C–E, G, *Elatocladus ginginensis* sp. nov.; detached planated foliage-bearing twigs; (C) UWA16703, x 1.5; (D) UWA118835, x 5; (E) UWA10466C, x 2; (G) UWA10464E, x 2; all from Bullsbrook Formation; F, H–K, *Carpolithes bullsbrookensis* sp. nov.; seed impressions and internal casts; (F) UWA10469F; (H) UWA104688; (I) UWA10462B; (J) UWA10469C; (K) UWA10469A; all from Bullsbrook Formation; all x 8.

mm, with a rounded or obtusely pointed apex and smooth surface apart from a prominent vertical ridge (on internal casts).

Description

Isolated seeds of indeterminate affinity. Seeds ovate to elliptical, reaching 5 mm wide, 7 mm long, wings absent; internal casts ovoid (Figures 9H–K). Prominent vertical ridge commonly evident on internal casts but surface otherwise lacks ornamentation (Figures 9F, J, K). Base truncate or rounded, apex rounded or closing to an obtuse point.

Comments

Seeds of this type are common in the Bullsbrook Formation and are frequently preserved in association with *Taeniopteris daintreei* leaves although no physical connection is evident. White (1981, 1986) figured similar though smaller seeds with a longitudinal ridge preserved in pentoxylalean (*Carnoconites*) cones from the Jurassic Talbragar fish beds in New South Wales. Seeds belonging to *Carnoconites cranwellii* Harris, 1962 fruits from the Victorian Early Cretaceous (Drinnan and Chambers 1985) are also substantially smaller (1 mm diameter) than the Western Australian seeds and differ by their polygonal outline. This may simply be due to crowding of seeds in the Victorian cones. Larger, more loosely packed *Carnoconites* cones may have borne more rounded seeds like White's (1981) examples from Talbragar. Seeds of *Carnoconites compactum* Srivastava, 1946 are similar in size although the species was defined upon permineralized material which does not clearly show the seed shape in lateral view (Sahni 1948; Vishnu-Mittre 1953). Compressed *Carnoconites laxum* Harris, 1962 fruits from New Zealand show only indistinct seeds not favourable for comparison to *Carpolithes bullsbrookensis*. *Carpolithes* sp. B of Bose and Banerji (1984) has a longitudinal ridge like *C. bullsbrookensis* but is much larger with an acute apex. Seeds belonging to *Rissikia talbragarensis* White, 1981 are of similar size to *C. bullsbrookensis* but lack a longitudinal ridge.

Winged conifer seed

Figure 10A

1993 Conifer seed with wing; McLoughlin and Guppy; figure 25.

Material

WAM P.89.191.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Seed positioned basally on wing, wrinkled, ovate, c. 3.5 mm wide, 5 mm long. A flange (<1 mm wide) around lateral margins of seed expands distally to form the 8.5 x 17 mm longitudinally striate oblong wing (Figure 10A).

Comments

The single available seed impression differs from those figured by Drinnan and Chambers (1986) from the Victorian Cretaceous by its distally expanded wing. The basal part of the seed has broken away leaving only a small portion of the fertile body. The seed does not show organic connections to any other plant remains and its affinities remain uncertain.

Genus *Bucklandia* Presl (in Sternberg), 1825

Type species

Bucklandia anomala (Stokes and Webb) Presl (in Sternberg), 1825; Jurassic; Sussex, England.

Bucklandia sp.

Figure 5E

1961 *Bucklandia* sp.; White; p. 305; plate 8, figure 2. [1961a].

1993 *Bucklandia*-type axis; McLoughlin and Guppy; p. 14; figure 9 (upper part).

Material

WAM P.96.8.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Axis impression bearing spirally arranged, broadly elliptical, leaf scars. Leaf scars 4 mm wide, 2 mm tall, lacking obvious vascular strands. Scars raised above surface of axis (on cast), separated by 0.5 mm grooves; arranged in 35° right-handed spirals, 50° left-handed spirals measured with respect to axial direction. Leaves and anatomical details not preserved.

Comments

The single stem fragment (upper right of Figure 5E) is similar to a number of Jurassic and Cretaceous axis casts assigned to *Bucklandia* Presl (in Sternberg), 1825. White (1961a) figured a larger axis from the same locality (Gantheaume Point, Broome) showing well developed spirally arranged elliptical leaf scars. The Western Australian examples lack the anatomical details necessary for

comparison to Indian *Bucklandia* species described by Seward (1917), Sahni (1932), Bose (1953a, b) and Sharma (1969a). Anatomically preserved *Bucklandia* axes have been associated with *Williamsonia* fructifications and *Ptilophyllum*-type foliage in India (Sahni 1932) suggesting a bennettitalean affinity. Although a *Roebuckia spatulata* frond occurs on the same slab as the *Bucklandia* specimen (Figure 5E), no connection is evident or inferred.

Ribbed axes

Figure 10B

1993 Striate axis; McLoughlin and Guppy; figure 23.

Material

WAM P.63.30, WAM P.65.38, WAM P.65.43, WAM P.65.46, WAM P.65.47, WAM P.65.48, WAM P.66.3, WAM P.66.4, WAM P.66.6, WAM P.66.7, WAM P.66.8, WAM P.66.9, WAM P.66.10, WAM P.66.12.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin (both Neocomian–Barremian).

Description

Several indeterminate longitudinally ribbed or striate axes are preserved as casts (figure 10B) and impressions. Axes reaching 4.5 cm wide, 13.5 cm long, cylindrical or flattened through compaction, commonly with external? longitudinal ribs averaging 2.5 mm apart. No axis nodes, attached leaves, fruits, or roots evident.

Comments

These axes lack diagnostic features necessary to assign them to any plant group, however, their size suggests that they may be the remains of a robust gymnosperm. The ribbed surface of some specimens invites comparison to equisetalean axes (e.g., Roy 1968; Drinnan and Chambers 1986), however, the Western Australian axes lack the transverse nodes typical of that group.

Genus *Rhizopteris* Schimper, 1869

Type species

Rhizopteris lycopodioides Schimper, 1869; Carboniferous; near Dresden, Germany.

Rhizopteris sp.

Figure 10C

Material

WAM P.89.184.

Distribution

Broome Sandstone (Neocomian–Barremian), Canning Basin.

Description

Irregular ?bifurcate axis bearing circular to elliptical protuberances set in surface depressions (on mould) separated by broad ridges and folds (Figure 10C). Protuberances reaching 3 mm wide, 7 mm long, roughly arranged along axis in *en echelon* bands. Sporangia, leaves, and cuticle not evident.

Comments

A single available specimen is similar to axes figured by Seward (1904) and Chapman (1909) from the Lower Cretaceous of Victoria. Chapman (1909) inferred a relationship between his *Rhizopteris* axes and *Taeniopteris* leaves. No such affinity can be deduced from the present material. The fossil probably represents a fern rhizome bearing circular to elliptical scars of abscissed frond rachises although no vascular traces are evident on the abscission zones. *Rhizopteris rajmahalensis* Gupta, 1955 is most closely comparable to the Broome Sandstone specimen but has C-shaped rather than circular to elliptical rachis scars. Bose (1958) figured additional material comparable to Gupta's (1955) specimens and considered that the axes belonged to conifers. Coniferous axes figured by Bancroft (1913) and Sahni (1931) have transversely elongate abscission scars in contrast to the oblique or longitudinally elongate scars of Gupta's (1955), Bose's (1958), or the Broome Sandstone *Rhizopteris* species.

Genus *Mesembrioxylon* Seward, 1919

Type species

Mesembrioxylon woburnense (Stopes) Seward, 1919; Cretaceous; Woburn, England.

Mesembrioxylon sp.

Figures 10D–H

1993 Silicified wood with *Teredo* burrow casts; McLoughlin and Guppy; figure 1.

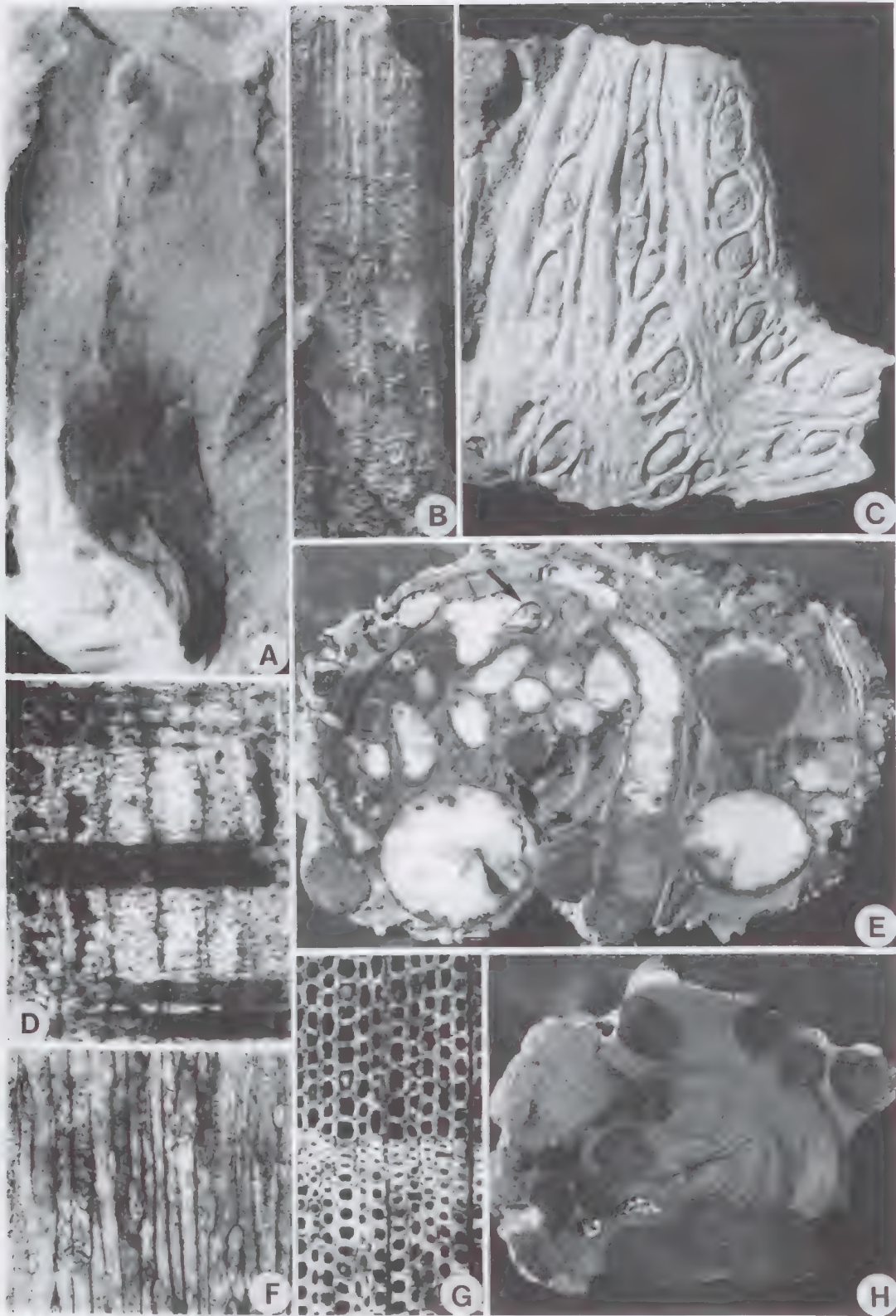
1994 Fossil wood; McLoughlin *et al.*; p. 453; figs 8a–m, 10a,b.

Material

UWA120186–UWA120237.

Distribution

The described specimens are derived from the Birdrong Sandstone (Neocomian–?Aptian), Carnarvon Basin. Other fossil woods have been reported from the Nanutarra Formation



(Neocomian–?Aptian) and Yarraloola Conglomerate (Neocomian–?Barremian) of the Carnarvon Basin, Dandaragan Sandstone (?Barremian–?Aptian) and Molecap Greensand (Cenomanian–Santonian) of the Perth Basin, and Nakina Formation (Barremian–lowermost Aptian) of the Collie Basin (Simpson 1912; Cox 1961; Playford *et al.* 1976; Hocking 1990, Buckhouse *et al.* 1995).

Description

Woods typically fragmentary, seldom exceeding 50 cm long and 15 cm diameter, randomly orientated in sediments. Woods show extensive biogenic borings (Figures 10E,H). Woods preserved by siliceous and phosphatic permineralization, strongly weathered and infiltrated by iron-oxide and clay minerals. Only secondary xylem tissues are preserved. Prominent growth banding evident (Figures 10G,H) but details of pitting arrangement on individual cell walls often poorly defined or absent (Figure 10D). Relatively sparse uniseriate xylem rays consist of 1–12 (av. 4) cells (Figure 10F). Uniseriate or rarely biseriate bordered pits are sparsely evident on radial walls of xylem tracheids. Tangential walls not pitted. Pits have oblique slit-like apertures where discernible. Growth bands variable in width (0.06–12 mm) both between and within specimens. False growth rings sporadically developed in some specimens. In most cases middle lamella (initially consisting of pectinoid compounds between the primary walls of adjacent cells) has been degraded producing a wood texture that appears to consist of detached or partially detached tracheids. Cambium, phloem, and bark tissues absent. Primary xylem and pith poorly preserved or masked by iron oxides.

Comments

The small pith content of the plants (pycnoxylic axes) suggests that the woods derive from the dominant arborescent elements of the Australian Early Cretaceous vegetation (*viz.*, the podocarp or araucarian conifers) rather than fern, pteridosperm, or bennettitalean groups that typically contain a large proportion of pith within the stem (manoxylic axes). Permineralized wood belonging to podocarp and araucarian conifers is common in Gondwanan Cretaceous sediments (Sahni 1931; Jefferson 1983; Francis 1986; Frakes and Francis 1990; Francis and Coffin 1992) and the foliage attributable to these

groups is abundant in coeval Western Australian strata. Identification of fossil conifer woods is largely based on pitting arrangements on the radial walls of longitudinal xylem tracheids and ray cells but due to poor preservation such details are not available for most Western Australian specimens. The absence of typically araucariacean closely spaced multiseriate hexagonal bordered pits on radial tracheid walls and sporadic presence of uniseriate bordered pits with oblique apertures suggests that these woods have podocarpacean affinities although cupressacean woods also have similar pitting arrangements (Greguss 1955). The prominent but variable growth banding and occasional development of false growth rings implies a distinctly seasonal climate but with considerable intra- and inter-seasonal variability (McLoughlin *et al.* (1994).

Cox (1961) illustrated infilled molluscan borings from the Nanutarra Formation (Early Cretaceous, Carnarvon Basin) both with and without traces of associated fossil wood. The casts are probably remnants of teredinid or pholadid boring casts left behind after the degradation of coniferous driftwood. One wood specimen in the Birdrong Sandstone assemblage shows a cross-section of an unidentified bivalve preserved within an excavation chamber (Figure 10E).

Saprophytic fungi

Figures 11A–I

1994 Fungi within wood; McLoughlin *et al.*; p. 455; figures 9a–l.

Material

UWA120187, UWA120217, UWA120228, UWA120229, UWA120231, UWA120232.

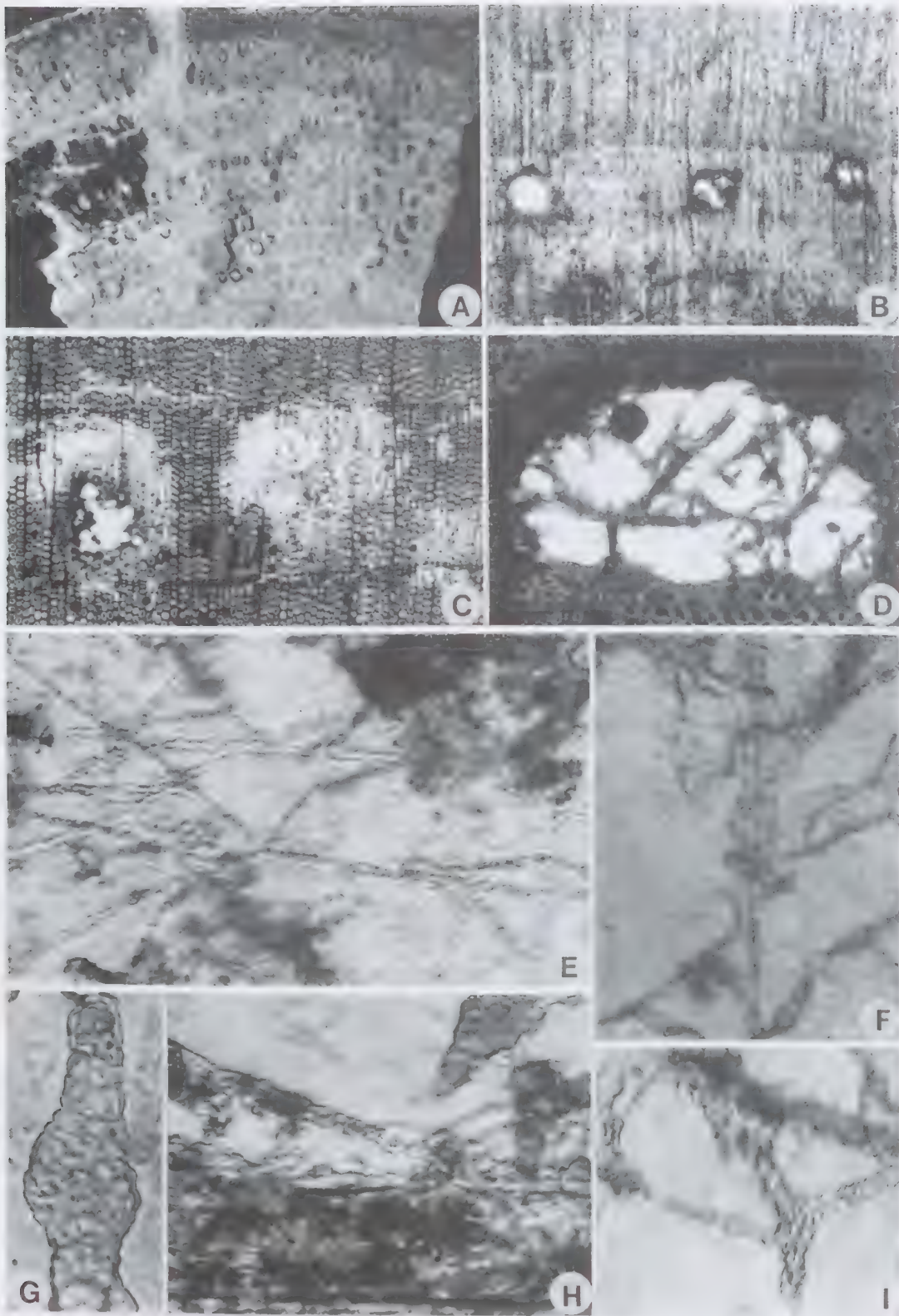
Distribution

Birdrong Sandstone (Neocomian–?Aptian), Carnarvon Basin.

Description

Several fossil wood specimens from the Birdrong Sandstone, Carnarvon Basin, show zones of partly degraded cells or cavities which are circular, elliptical, or irregular in transverse section and elliptical in longitudinal section. The cavities are up to 4 mm in axial length and 0.2–0.9 mm in

◀ **Figure 10** **A**, Winged seed with portions of base and apex removed; WAM P.89.191; Broome Sandstone; x 6; **B**, Cast of ribbed axis; WAM P.63.30; Broome Sandstone; x 1; **C**, *Rhizomopteris* sp.; WAM P.89.184; Broome Sandstone; x 2; **D,F,G**, *Mesembrioxylon* sp.; (D) radial section with three groups of ray cells, UWA120187, x 60; (F) tangential section showing rays generally comprising 2–4 cells, UWA120199, x 30; (G) transverse section showing transition from latewood (bottom) to earlywood (top), UWA120186, x 30; all from Birdrong Sandstone; **E,H**, Transverse sections of *Mesembrioxylon* wood showing variation in growth rings and intensive bivalve borings filled by calcite and/or glauconitic sand. Note preserved bivalve within bored cavity (E: arrowed); (E) UWA120220, x 2; (H) UWA120208, x 1.5; both from Birdrong Sandstone.



diameter. The degraded zones occur commonly, though not exclusively, within the latewood (Figures 11A,B,C). The cavities are either filled with secondary iron oxides or silica or occasionally contain ramifying weakly septate filaments reaching 450 µm in length and 4–15 µm in width (Figure 11D). The filaments branch irregularly, have an external bullate texture, and appear to contain irregularly spaced and poorly defined septa (Figures 11E–G,I). Filaments often occur in intimate contact with the degraded wood cells of the cavity margin (Figure 11F).

Comments

Such filaments and spindle-shaped wood cavities are morphologically similar to saprophytic fungal hyphae and white pocket rot cavities described from other modern and fossil woods (Blanchette 1980; Stubblefield *et al.* 1985; Stubblefield and Taylor 1986, 1988; Weaver *et al.*, in press). Jefferson (1987) figured fungal hyphae and possible spores in Early Cretaceous conifer wood from Alexander Island, Antarctica, and Halle's (1913) sketch of Mesozoic fossil wood from the Antarctic Peninsula also shows elliptical markings reminiscent of pocket rot. The Birdrong Sandstone woods incorporate the first examples of fossilized saprophytic fungi recorded from Western Australia (McLoughlin *et al.* 1994).

Other plant remains

White (1961a) figured a number of Western Australian plant macrofossils many of which have been reassigned here to different taxa on the basis of information from new material in the Western Australian Museum and University of Western Australia collections (Table 1). However, a few of her figured specimens are not matched by conspecific material in the Western Australian collections. Her *Pagiophyllum peregrinum* Schimper from the Callawa Formation, although similar to *Araucaria* sp. B, has leaves with distinctly mucronate apices. White's (1961a, plate 6, figure 4) "fine frond" is too incomplete for confident identification but it may represent the fragmentary remains of an *Aculea* or *Sphenopteris* frond or an *Elatocladus* terminal twig. Her *Pachypteris* sp., also

from the Callawa formation, is a pinna bearing oblanceolate pinnules some of which appear to have elliptical fertile bodies along their acroscopic margins. Similar fronds from the Victorian and Indian Early Cretaceous have been assigned to *Onychiopsis paradoxus* Bose and Sukh Dev, 1961 (Drinnan and Chambers 1986). White's (1961a) *Cladophlebis albertsi* (Dunker) from the Leveque Sandstone [now regarded as part of the Broome Sandstone (Yeates *et al.* 1984)] differs from *Cladophlebis* sp. cf. *C. oblonga* by its pointed pinnules but her specimen is too poorly preserved for close comparison to other described species. White's (1961a) *Dichopteris delicatula* Seward from the Broome Sandstone does not have preserved venation and may be a *Sphenopteris* or *Cladophlebis* species. Her *Nilssonia schaumbergensis* Dunker, also from the Broome Sandstone has pinnules of variable width. The specimen may be a *Taeniopteris daintreei* leaf showing irregular lamina dissection like some forms illustrated herein. White's *Cycadolepis* sp. from the Cronin Sandstone is too poorly preserved for definite identification. White (1961a) also mentions but does not figure several other plant taxa from the Canning and Officer Basin Lower Cretaceous including: *Carpolithus circularis*, *Cladophlebis* sp., *Taeniopteris howardensis* Walkom, *Dictyophyllum davidi* Walkom, *Pterophyllum* sp., *Sphenopteris superba* Shirley, *Brachyphyllum mamillare* Lindley and Hutton, and *Ginkgoites digitata* Brongniart. These identifications (Table 1) have not been assessed in the present study.

Walkom (in McWhae *et al.* 1958) identified specimens referable to *Nilssonia*, *Otozamites*, and *Elatocladus* from the Nanutarra Formation. The whereabouts of this material is unknown and no revision of the identifications can be attempted. However, these genera are common elements of the Early Cretaceous Broome Sandstone flora and it is likely that several species are shared between these formations. Walkom (in McWhae *et al.* 1958) also reported fossil leaves from the Yarraloola Conglomerate (Early Cretaceous, Carnarvon Basin) but provided no identifications and the location of his specimens is unknown prohibiting systematic re-evaluation.

Brunnschweiler (in Traves *et al.* 1956) tentatively

◀ **Figure 11** Aspects of fungal attack on, and hyphae preservation within, *Mesembrioxylon* (conifer) wood from the Birdrong Sandstone. (A) UWA120231, transverse section of wood showing fungal-degraded pockets, x 2. (B) UWA120187, transverse section of wood showing fungal-degraded pockets positioned within latewood, x 6; (C) UWA120221, transverse section of wood showing initial stages of cell breakdown and pocket formation, x 12; (D) UWA120186, details of a pocket with numerous phosphate coated fungal hyphae and a spherical body (upper left), x 60; (E) UWA120217, branched hyphae within a pocket, x 60; (F) UWA120232, details of fungal hyphae represented by a thin central filament surrounded by a bullate-textured phosphate coating, x 120; (G) UWA120186, details of an expanded area near the tip of a fungal hypha, x 600; (H) UWA120132, fungal hyphae in contact with wood tracheids along the margin of a pocket, x 120; (I) UWA120232, branched fungal hyphae in pocket, x 120.

Table 1 Tentative revision of Lower Cretaceous plants illustrated or identified by White (1961a) from Canning and Officer Basins collections compiled during regional geological surveys of the 1950s and 1960s.

White's (1961a) identification/ illustration	Formation	Tentative revised identification
<i>Stenopteris tripinnata</i> Walk. (Pl. 4, fig. 6)	Cronin Sst	cf. <i>Aculea bifida</i>
<i>Linguifolium denmeadi</i> Jones and de Jersey (Pl. 5, fig. 3)	Cronin Sst	<i>Phyllopteroides westralensis</i>
' <i>Neorhachopteris minuta</i> ' (Pl. 5, fig. 4)	Callawa Fm	<i>Sphenopteris</i> sp. A
<i>Pagiophyllum peregrinum</i> Sch. (Pl. 5, fig. 5)	Callawa Fm	? <i>Araucaria</i> sp.
<i>Ruffordia mortoni</i> Walk. (Pl. 5, figs 6,7)	Callawa Fm	cf. <i>Sphenopteris</i> sp. A
<i>Elatocladus planus</i> (Feist.) (Pl. 6, figs 1A, 2A)	Cronin Sst	<i>Elatocladus ginginensis</i>
<i>Taeniopteris</i> cf. <i>elongata</i> Walk. (Pl. 6, figs 1B, 2B)	Cronin Sst	<i>Taeniopteris daintreei</i>
<i>Ptilophyllum pecten</i> (Phillips) (Pl. 6, fig. 1D; Pl. 8, fig. 1)	Cronin Sst, Broome Sst	<i>Ptilophyllum cutchense</i>
<i>Cycadolepis</i> sp. (Pl. 6, fig. 2C)	Cronin Sst	not identified
stem (Pl. 6, fig. 3)	Callawa Fm	<i>Nathorstianella babbagensis</i>
fine frond (Pl. 6, fig. 4)	Callawa Fm	not identified
<i>Pachypteris</i> sp. (Pl. 6, fig. 5)	Callawa Fm	<i>Onychiopsis</i> sp.
<i>Cladophlebis australis</i> (Morr.) (Pl. 7, figs 1,6)	Callawa Fm, Broome Sst	<i>Cladophlebis</i> cf. <i>oblonga</i>
<i>Cladophlebis albertsi</i> (Dunk.) (Pl. 7, fig. 2)	Broome Sst	? <i>Cladophlebis</i> sp.
<i>Dichopteris delicatula</i> Sew. (Pl. 7, fig. 3)	Broome Sst	? <i>Sphenopteris</i> or <i>Cladophlebis</i> sp.
<i>Nilssonsonia schaumbergensis</i> Dunk. (Pl. 7, fig. 4)	Broome Sst	<i>Nilssonsonia</i> or <i>Taeniopteris</i> sp.
<i>Otozamites bengalensis</i> O. and M. (Pl. 7, fig. 5)	Broome Sst	<i>Ptilophyllum cutchense</i>
<i>Bucklandia</i> sp. (Pl. 8, fig. 2)	Broome Sst	<i>Bucklandia</i> sp.
<i>Zamites</i> sp. (Pl. 8, fig. 3)	Broome Sst	<i>Ptilophyllum acutifolium</i>
<i>Hausmannia</i> cf. <i>buchii</i> Andrae (Pl. 8, fig. 4)	Broome Sst	<i>Hausmannia</i> sp.
<i>Taeniopteris</i> sp.	Cronin Sst	not assessed
<i>Carpolithus circularis</i>	Cronin Sst	not assessed
<i>Hausmannia</i> sp.	Cronin Sst	not assessed
<i>Cladophlebis</i> sp.	Broome Sst	not assessed
<i>Taeniopteris howardensis</i> Walk.	Broome Sst	not assessed
<i>Dictyophyllum davidi</i> Walk.	Broome Sst	not assessed
<i>Pterophyllum</i> sp.	Broome Sst	not assessed
<i>Sphenopteris superba</i> Shirley	Broome Sst	not assessed
<i>Brachyphyllum mamillare</i> L. and H.	Broome Sst	not assessed
<i>Ginkgoites digitata</i> Brongn.	Callawa Fm	not assessed
<i>Brachyphyllum foliage</i>	Callawa Fm	not assessed

identified ?*Johnstonia*, *Ginkgo*, *Cladophlebis*, *Pagiophyllum*, ?*Brachyphyllum*, *Taeniopteris*, *Sphenopteris*, ?*Samaropsis*, *Dictyophyllum* and indeterminate wood from the Callawa Formation, Canning Basin. The presence of *Johnstonia* (= *Dicroidium*) would denote a Triassic age for this unit but the identification is probably incorrect.

Brunnschweiler (1960) listed but did not describe or illustrate the following taxa from the Broome Sandstone at Gantheaume Point: *Ptilophyllum pecten*, *Cladophlebis australis*, *Otozamites* cf. *bengalensis*, *Pseudocycas* sp., *Hausmannia* sp., ?*Cordaite* sp., *Pterophyllum* sp., ?*Microphylopteris* sp., *Sphenopteris* cf. *superba* Walkom, ?*Dictyophyllum* sp., *Cladophlebis* cf. *albertsi*, *Taeniopteris* cf. *howardensis*, and *Nilssonsonia* sp. Most of these taxa are probably attributable to species described herein. The identification of *Cordaite*, a Palaeozoic genus, is almost certainly incorrect. The *Dictyophyllum* specimens may represent fragmentary portions of *Hausmannia* fronds although the former is not uncommon in the Indian

late Mesozoic (Bose and Jana 1979; Bose and Banerji 1984). Specimens referred to *Otozamites*, *Pterophyllum* and *Pseudocycas* may belong to one of the *Ptilophyllum* species described above.

Comparisons between the Western Australian assemblages

A significant number of plant taxa are shared between the various Western Australian Early Cretaceous formations (Table 2). Although there is evidence of intra-Australian floral provincialism in the Early Cretaceous (Dettmann *et al.* 1992), the Western Australian marginal basins all lay within latitudes of about 45°–55° during that period (Veevers *et al.* 1991) and probably experienced similar climatic conditions. Minor differences between the Western Australian assemblages are probably attributable to limited sampling, local depositional factors and environmental setting. For example, the fully fluvial Cronin Sandstone appears to contain a higher representation of gymnosperms than units deposited in deltaic or

Table 2 Distribution of fossil plant taxa in the studied stratigraphic units. See text for author citations.

SPECIES	LEEDERVILLE FORMATION	BULLSBROOK FORMATION	NANUTARRA FORMATION	BIRDROG SANDSTONE	BROOME SANDSTONE
<i>Isoetes elegans</i>	+				
<i>Nathorstianella babbagensis</i>					+
<i>Hausmannia</i> sp.					+
<i>Cladophlebis</i> cf. <i>oblonga</i>		+			+
<i>Phyllopteroides westralensis</i>		+			+
<i>Microphylopteris gleichenioides</i>					+
<i>Roebeckia spatulata</i>					+
<i>Aculea bifida</i>					+
<i>Sphenopteris warragulensis</i>					+
<i>Sphenopteris</i> sp. A					+
<i>Thinnfeldia</i> cf. <i>talbragarensis</i>	+	+			
<i>Taeniopteris daintreei</i>	+	+			+
Pinnate frond		+			
<i>Nilssonia</i> sp. A			+		
<i>Nilssonia</i> sp. B					+
<i>Ptilophyllum acutifolium</i>			+		+
<i>Ptilophyllum cutchense</i>	+	+			+
<i>Ptilophyllum boolensis</i>					+
<i>Zamites</i> sp.		+			
<i>Araucaria</i> sp. A					+
<i>Araucaria</i> sp. B					+
<i>Araucaria</i> sp. C					+
Araucarian cones					+
Araucarian cone scales					+
<i>Elatocladus ginginensis</i>	+	+			+
<i>Carpolithes bullbrookensis</i>		+			
Winged conifer seeds					+
<i>Bucklandia</i> sp.					+
Ribbed axes		+			+
<i>Rhizomopteris</i> sp.					+
<i>Mesembrioxylon</i> sp.				+	
Saprophytic fungi				+	

coastal plain environments. The latter units are richer in lycophytes and pteridophytes probably owing to milder local maritime climates and wetter riparian environments, or higher water tables in lowland settings.

Relationships with other Australian floras

Other significant Australian mid- to late Mesozoic floras include the Gippsland–Otway Basin assemblages of Victoria (Douglas 1969, 1973; Drinnan and Chambers 1986), the Talbragar flora of New South Wales (Walkom 1921a; White 1981), the Eromanga, Clarence–Moreton, Laura, Styx, and Maryborough Basin floras of Queensland (Walkom 1917a,b, 1918, 1919a, 1928; Hill *et al.* 1966; Gould 1978, 1980; McLoughlin and Drinnan 1995; McLoughlin *et al.* 1995), the Bauhinia Downs flora of the Northern Territory (White 1961b), the Mt Babbage flora of South Australia (Glaessner and Rao 1955), and the Mingenev (Yarragadee

Formation) flora of Western Australia (Arber 1910; Walkom 1921b). Of these, the Otway, Gippsland, and Eromanga Basin floras are the best known.

Douglas (1969, 1971) proposed four assemblage zones (Zones A–D) for Victorian Neocomian to Early Albian strata based on plant macrofossils and tied these to the independent palynostratigraphic zonation of Dettmann (1963); later refined by Dettmann and Playford (1969), Dettmann and Douglas (1976), and Helby *et al.* (1987). Douglas’ (1969) megafloal zones are largely based on the presence or absence of key foliage species hence their recognition may be strongly influenced by local palaeoenvironmental, depositional, and seasonal factors. The collective Western Australian assemblages bear greatest similarity to Douglas’ (1969) Zone B (Neocomian) flora due to the presence of the key species *Taeniopteris daintreei* and *Ptilophyllum boolensis*. *Phyllopteroides westralensis* is an entire-margined form similar to *P.*

laevis from the Victorian Zone B (and equivalent strata in Queensland). This favours an Early Cretaceous age but *P. westralensis* requires further study to determine its phylogenetic relationships with the range of eastern Australian species. Another diagnostic Victorian Zone B species, *Pachypteris austropapillosa* is absent from the Western Australian assemblages although a poorly preserved pinnate frond from the Bullsbrook Formation (Figure 6D) may be a related form.

Douglas's (1969) latest Jurassic or earliest Cretaceous Zone A floras are characterized by bennettitalean leaf forms not recognized in Western Australia. Victorian Zone B floras are also rich in bennettitaleans but only one Western Australian form (*Ptilophyllum boolensis*) is shared suggesting significant intra-Australian floristic provincialism. Nevertheless, the abundance of bennettitaleans in Zone B suggests better correlation with the Western Australian floras than does the succeeding Zone C where bennettitaleans are entirely absent. The Victorian Zone C (?late Neocomian to early Albian) floras also differ from the Western Australian assemblages by the presence of ginkgophytes, sphenophytes, angiosperms, and a range of distinctive pteridophyte and conifer species (Drinnan and Chambers 1986). A few species (*Taeniopteris daintreei*, *Sphenopteris warragulensis*, and *Aculea bifida*) are shared between these assemblages but some of these forms may be long-ranging. Douglas' (1969) Zone D (middle–?late Albian) floras are dominated by conifer and fern species which are not represented in Western Australia. Australian Cenomanian floras mark the decline of many gymnosperm groups and diversification of the angiosperms (McLoughlin *et al.* 1995).

The Talbragar Fish Bed flora (Merrygoen Ironstone Member of the Purlawaugh Formation) illustrated by Walkom (1921a) and White (1981) is generally regarded as late Early Jurassic in age (Hind and Helby 1969; Gould 1975) but contains a number of superficially similar plant fossils to the Western Australian Early Cretaceous assemblages including species of *Taeniopteris*, *Thinnfeldia*, *Brachyphyllum* (*Araucaria* herein), *Nilssonina*, and *Rissikia* (= *Elatocladus*). However most forms can be distinguished at species level and the generic similarities may be due to palaeoecological similarities between these assemblages. The Early and Middle Jurassic floras of the Marburg Formation, Walloon Coal Measures, and equivalents in the Clarence–Moreton Basin of New South Wales and Queensland (Walkom 1915, 1917a,b, 1919b; Hill *et al.* 1966; Gould 1971, 1980; McLoughlin and Drinnan 1995) also share several genera with the Western Australian Cretaceous assemblages but clear species-level distinctions are apparent. Plant assemblages from the Dalrymple

Sandstone, Laura Basin, initially assigned to the Cretaceous by Walkom (1928) are now regarded as Jurassic in age (Gould 1975) and only share one species (*Microphyllopteris gleichenioides*) with the Western Australian assemblages. The Middle to Late Jurassic floras of the Yarragadee Formation, Perth Basin, Western Australia (Arber 1910; Walkom 1921a; McLoughlin and Hill, in press) contain *Otozamites* fronds and *Pagiophyllum* branchlets that differ from the Early Cretaceous fossils. Several other fragmentary plant fossils have been recorded from the Yarragadee assemblages but the flora requires systematic revision.

A small plant assemblage of probable Late Jurassic age from the Hooray Sandstone in the northwestern Eromanga Basin, Northern Territory (Gould 1978), is dominated by Bennettitalean fronds (*Ptilophyllum* sp.) and conifer twigs but no species are shared with the Western Australian Cretaceous floras.

The Maryborough Formation of the Maryborough Basin, Queensland, contains a small macroflora showing some similar elements [*Taeniopteris* spp., *Ptilophyllum pecten* (= *?Ptilophyllum cutchense*)] to the Western Australian assemblages (Walkom 1918). However, the Maryborough Formation floras are more similar to the Gippsland Basin Zone C (?late Neocomian to earliest Aptian) macrofloras in terms of the conifer, ginkgophyte and equisetalean groups represented.

The Albian Burrum Coal Measure flora from the Maryborough Basin (Walkom 1919a) has a number of generic similarities to Western Australian assemblages but there are few conspecific elements. The presence of angiosperms and ginkgophytes in the Burrum flora suggests closer correlation with the Victorian Zone C–D floras. Similarly, the Styx Coal Measures of central Queensland are also characterized by the presence of angiosperms and are probably of Albian age (Walkom 1919a; Dettmann and Playford 1969; Dettmann and Douglas 1976).

The little-studied Stanwell Coal Measures west of Rockhampton, Queensland, are associated with marine strata yielding Neocomian bivalves (Skwarko 1968 and early to middle Albian palynofloras (Dettmann and Playford 1969). They also contain a macroflora consisting of *Equisetites* sp., *Cladophlebis* sp., *Phyllopteroides laevis*, *Taeniopteris* spp. (cf. *Taeniopteris daintreei*), *Ptilophyllum pecten* (cf. *Ptilophyllum cutchense*), *Araucarites polycarpa* Tenison-woods, and *Elatocladus plana* (cf. *Elatocladus ginginensis*), showing strong similarities to the Western Australian assemblages (Walkom 1915, 1917a,b; Hill *et al.* 1966; Cantrill and Webb 1987). Cantrill and Webb (1987) suggested a Neocomian age for the Stanwell Coal Measures owing to the occurrence of the index fossil *Phyllopteroides laevis*

and its distribution in Neocomian strata of the Surat and Gippsland Basins.

The floras most closely comparable to the Western Australian assemblages are those from the Algebuckina Sandstone (Eromanga Basin) at Mt Babbage, South Australia, and from the Lees Sandstone and overlying beds (Carpentaria Basin), at Bauhinia Downs, Northern Territory. The Algebuckina Sandstone incorporates Middle Jurassic to Neocomian sediments (Moore 1986; Wiltshire 1989). The macrofloras at Mt Babbage occur in the upper part of this unit and are probably of Neocomian age. Although requiring systematic revision, the Mt Babbage flora shares several taxa with the Western Australian assemblages (Glaessner and Rao 1955). Most notable are the co-occurrences of *Nathorstianella babbagenis*, *Ptilophyllum cutchense*, and *Taeniopteris daintreei*. (White 1961b, 1966). The Bauhinia Downs flora likewise shares several key taxa with Western Australia including *Ptilophyllum cutchense*, *Microphylopteris gleichenioides*, *Hausmannia* sp., and *Taeniopteris daintreei*, and owing to the abundance of bennettitaleans and lack of ginkgophytes, is of probable Neocomian rather than Aptian age as suggested by Dettmann *et al.* (1992).

A Neocomian–Barremian age is proposed for the collective Western Australian terrestrial plant assemblages described here. Accumulation of plant remains in several regions along the continent's western margin during the Neocomian–Barremian probably occurred as part of a single phase of widespread fluvio–deltaic sedimentation associated with continental breakup, marginal basin sag, and regional and global sea-level fluctuations at that time (McLoughlin, *et al.* 1994).

Comparisons with other Gondwanan floras

The Western Australian Cretaceous floras share several genera and possibly some species with the Rajmahal, Kutch, and Jabalpur floras of India. The Rajmahal Series has been variously assigned to: the lower, middle, or upper Jurassic according to traditional palaeobotanical studies (Feistmantel 1877a; Halle 1913; Sahni and Rao 1933); the Lower Cretaceous based on palynostratigraphy (Playford and Cornelius 1967); and the Albian according to radiometric (K–Ar) dating (McDougall and McElhinny 1970). Sukh-Dev (1987) re-evaluated the stratigraphic relationships of the Indian Mesozoic macrofloras and established 12 assemblage zones from the Early Triassic to latest Cretaceous. He reassigned the lower Rajmahal assemblages to the Lower Cretaceous. Sukh-Dev's (1987) *Dictyozamites–Pterophyllum–Anomozamites* Assemblage Zone corresponds most closely to the Western Australian Cretaceous floras by its high proportion of bennettitaleans, *Taeniopteris*, and the occurrence of comparable species of ferns

[*Gleichenites* (= *Microphylopteris*), *Hausmannia*, and *Cladophlebis*] and Conifers [*Araucaria*, *Araucarites* (cone scales and cones), and *Elatocladus*]. This Indian zone differs from the Western Australian assemblages by its possession of ginkgophyte and *Pachypteris* species and its lack of *Phyllopteroides*, *Roebuckia*, and *Nathorstianella* species. The *Dictyozamites–Pterophyllum–Anomozamites* Assemblage Zone is best represented in the Jabalpur Formation (Chaugan Forest district) of Madhya Pradesh (Crookshank 1936), the Lower Rajmahal Formation (intertrappean beds 1–3, Rajmahal Hills) of Bihar (Bose and Sah 1968; Sharma 1969b, 1971, 1975; Zeba-Bano *et al.* 1979), and the lower Bhuj Formation of Kutch (Bose and Banerji 1984) together with a number of lesser-studied units in peninsula India, Sri Lanka, and Nepal (see Sukh-Dev 1987). Certain genera (and perhaps species) from Sukh-Dev's (1987) succeeding *Allocladus–Brachyphyllum–Pagiophyllum* Assemblage Zone and *Weichselia–Onychiopsis–Gleichenia* Assemblage Zone are also shared with the Western Australian floras but these assemblages appear to be more akin to the Victorian Zone C (?late Neocomian–early Albian) floras.

The Tico (Baqueró Formation) Flora of Patagonia (Argentina) has a number of conifer, fern, and bennettitalean genera in common with the Western Australian Cretaceous floras (Herbst 1962a; Archangelsky 1963a,b,c, 1964a,b; Archangelsky and Baldoni 1972) but the number of shared taxa are fewer than between the Western Australian and Indian assemblages. The Baqueró Formation has been assigned a late Barremian to early Aptian age based on its palynoflora (Archangelsky *et al.* 1984) and most notably differs from the Western Australian Early Cretaceous assemblages by its possession of angiosperm remains (Archangelsky 1963c; Romero and Archangelsky 1986). It probably has greater floristic affinities with the Victorian Zone C assemblages.

A number of other lesser-studied Early Cretaceous floras from Argentina show distinct similarities to the Western Australian assemblages. Though dated as Aptian on the basis of associated ammonoid faunas, the Kachaike Formation, Santa Cruz, has yielded *Microphylopteris*, *Hausmannia*, *Cladophlebis*, and *Ptilophyllum* species strikingly similar to those from the Broome Sandstone (Longobucco *et al.* 1985). The Apeleg Formation, Chubut, also contains species of *Taeniopteris*, *Cladophlebis*, and *Ptilophyllum* similar to those from Western Australia and has been assigned a Hauterivian–Barremian age (Baldoni and de Vera 1980). Although some elements (e.g., *Ticoa*, *Zamites*, and *Cycadolepis* spp.) differ, the Spring Hill Formation of southern Argentina and Chile also has a number of bennettitaleans, ferns, and

conifers, which are comparable to Western Australian taxa, and has been assigned an Early Cretaceous (probable Hauterivian–Barremian) age (Archangelsky 1976; Baldoni 1979, 1980c; Baldoni and Taylor 1983).

Macrofloras from the South African Kirkwood, Mngazana, and Makatini Formations range from Berriasian to late Aptian in age and are represented by *Marchantites*, *Ricciopsis*, *Cladophlebis*, *Sphenopteris*, *Onychiopsis*, *Taeniopteris*, *Pseudoctenis*, *Zamites*, *Dictyozamites*, *Araucaria*, and *Podocarpus* species (Anderson and Anderson 1985). Most of these are readily distinguishable from Australian forms, a few are shared with South American assemblages but the majority appear to be endemic to South Africa suggesting an early floristic separation of this province from other Gondwanan regions.

The upper Fossil Bluff Formation flora (Barremian–Albian) of Alexander Island, Antarctica, contains *Hausmannia*, *Cladophlebis*, *Taeniopteris*, and *Elatocladus* species comparable to those in the Western Australian assemblages but differs in its possession of ginkgophytes, *Pagiophyllum*, *Bellarinea*, and *Phlebopteris*. The upper Fossil Bluff Formation floras correspond more closely with the Victorian Zone C assemblages. The Hope and Botany Bay floras of the Antarctic Peninsula were originally regarded as Jurassic in age (Halle 1913). Later studies suggested an Early Cretaceous age (Francis 1986; Gee 1989) based on an abundance of sphenopterid, cladophlebid, taeniopterid, bennettitalean, and podocarpacean remains similar to other Gondwanan Early Cretaceous assemblages. However, these Antarctic assemblages are characterized by the presence of possible sagenopterid pteridosperms and *Goeppertella* favouring an Early Jurassic age (Rees 1993).

Comparisons with extra-Gondwanan floras

Many plant families have wide, often cosmopolitan, distributions in the Jurassic, however, by Early Cretaceous times fragmentation of Pangaea led to renewed floral provincialism equivalent to that of the late Palaeozoic (Meyen 1987). Although some families and genera maintained wide distributions in the Early Cretaceous, Gondwanan floras are readily distinguishable from those of other provinces at species (and often genus) level. Geographically, the closest extra-Gondwanan landmasses to Australia during the Early Cretaceous were probably the series of disjunct terranes presently constituting South China, Indochina, and Malesia (Audley-Charles 1988; Metcalfe 1991). Although Mesozoic floras have been reported from these areas (Kimura and Ohana 1992), many have not yet been fully documented. Late Jurassic and Early Cretaceous

floras of Japan are distinguished from Australian floras by the presence of, or greater representation of, bennettitalean taxa such as *Zamites*, *Neozamites*, *Anomozamites*, *Dictyozamites*, *Ctenozamites*, cycadales (such as *Ctenis*), czekanowskialeans, and conifers including *Podozamites*, *Cupressinocladus*, and *Frenelopsis* (Kimura and Ohana 1987a,b,c, 1992, 1988, 1989; Kimura *et al.* 1985, 1991, 1992). Malayan and Thai mid- to late Mesozoic floras (Kon'no 1967, 1972; Smiley 1970; Kon'no and Asama 1975; Asama *et al.* 1981) and coeval Indochinese macrofloras (Serra 1963, 1966; Vozenin-Serra 1977) have affinities with other southern (Ryoseki-type) east Asian floras (Kimura 1987, 1988) and have few if any elements in common with Australian assemblages.

Palaeoenvironments and palaeoclimates

The presence of high latitude forests and terrestrial vertebrate populations together with oxygen isotope signatures from marine invertebrates suggest globally raised temperatures during the Early and mid-Cretaceous (Frakes 1979; Douglas and Williams 1982; Barron 1983; Spicer and Parish 1986; Rich and Rich 1989; Frakes and Francis 1990). Various factors including reduced obliquity of the Earth's rotational axis, palaeogeographic configurations of continents and ocean currents, higher atmospheric CO₂ levels, and increased levels of solar radiation have been suggested as possible causes for the apparently high palaeotemperatures (Douglas and Williams 1982; Creber and Chaloner 1985; Barron 1983, 1984). Palaeomagnetic evidence (Veevers *et al.* 1991) indicates that the Early Cretaceous Western Australian floras existed in middle latitudes (45°–55°) within presumably warmer climates than those experienced by the higher palaeolatitude Victorian and Antarctic floras (Douglas 1969, 1973; Jefferson 1983). However, fossil woods from the Birdrong Sandstone show well-defined growth rings consistent with a distinctly seasonal climate. Analysis of 48 permineralized conifer wood samples from the Giralial Anticline, Carnarvon Basin (McLoughlin *et al.* 1994), showed mean sensitivity values in the range of 0.148 to 0.673 [i.e. complacent to strongly sensitive (Fritts 1976)] with an average mean sensitivity of 0.348 (moderately sensitive). These growth indices together with the presence of sporadic false growth rings within the woods suggest a pronounced seasonal climate but with substantial inter-seasonal variability in environmental parameters.

The presence of matted *Taeniopteris daintreei* leaves in the Bullsbrook Formation suggests a deciduous or semi-deciduous habit for these pentoxylaleans consistent with evidence from the Victorian Cretaceous (Douglas and Williams 1982; Drinnan and Chambers 1986) which suggests that

these plants were adapted to a seasonal climatic regime. A deciduous habit for other plant groups in the Western Australian assemblages is less obvious although the complete and sometimes matted fronds of bennettitaleans such as *Ptilophyllum cutchense* in the Broome Sandstone may reflect deciduousness.

The range of fern and lycophyte species in the collections suggests a humid microthermal to megathermal climate based on the distributions of related extant taxa. However, most of the fossiliferous units were deposited in lowland deltaic environments where high water table (rheotrophic) rather than necessarily high rainfall (ombotrophic) conditions may have aided the growth of pteridophytes. Modern cycadophytes typically grow in mesothermal to megathermal conditions and most forms probably occupied similar climates in the past (Douglas and Williams 1982). The abundance of bennettitalean foliage in the studied assemblages favours interpretation of a relatively warm (though seasonal) climate. Some of the bennettitaleans have comparatively small fronds (e.g., *Ptilophyllum boolensis*) which may have been a foliar response to local water stress.

Differential representation of plant groups between the various Western Australian Neocomian–Barremian assemblages is relatively minor and probably reflects local differences between depositional settings (e.g., alluvial valley versus coastal environments). The Nanutarra Formation yields a small macroflora mixed with a marine invertebrate fauna (Cox 1961) and was probably deposited within paralic to shallow marine conditions. The coastal to nearshore sediments of the Birdrong Sandstone lack leaf remains but contain abundant mollusc-bored fossil wood, ammonoids, and marine vertebrates (McLoughlin *et al.* 1994). Whilst some of the plant remains in the Broome Sandstone are clearly allochthonous, autochthonous root beds and *Nathorstianella* corms are evident in exposures at Gantheaume Point, Broome. This coarse-grained unit also contains diverse dinosaurian trackways (Long 1990) and sparse bivalves (Yeates *et al.* 1984) and was probably deposited within a deltaic setting. The plant-bearing Callawa Formation and Cronin Sandstone, although not examined during this study, lack invertebrate fossils and were probably deposited within proximal fluvial (alluvial valley/ alluvial plain) settings. The Leederville Formation consists of interbedded sandstones, siltstones, and claystones and was deposited within paralic to shallow marine environments (Cockbain 1990). The correlative Bullsbrook Formation is dominantly composed of sandstone but contains local plant-bearing overbank shale lenses and was deposited within fluvial environments (Cockbain 1990).

CONCLUSIONS

Thirty-two fossil plant and fungi taxa have been described from five Early Cretaceous lithostratigraphic units in Western Australia. Four new species (*viz.*, *Phyllopteroides westralensis*, *Roebuckia spatulata*, *Elatocladus ginginensis*, and *Carpolithes bullsbrookensis*) are defined while several others are described under open nomenclature owing to insufficient or inadequately preserved material prohibiting comparisons to established taxa. The fossil assemblages comprise lycophytes, ferns, pteridosperms, pentoxylaleans, bennettitaleans, and araucarian and podocarpacean conifers. Bennettitaleans, pentoxylaleans, and conifers are the numerically dominant elements of the flora. Macrofossil suites from the Broome Sandstone (Canning Basin), Nanutarra Formation and Birdrong Sandstone (Carnarvon Basin), and Leederville and Bullsbrook Formations (Perth Basin) are correlated with Douglas' (1969) *Ptilophyllum–Pachypteris austropapillosa* Zone (Zone B) of Victoria and indicate a Neocomian–Barremian age. The Nanutarra Formation is a diachronous marginal marine to paralic unit and its age may locally extend to the Aptian based on invertebrate assemblages (Cox 1961). The Western Australian Early Cretaceous floras are most closely comparable with coeval assemblages from South Australia and the Northern Territory. Lesser similarities are evident with eastern Australian and Indian floras and fewer species are shared with South America, Antarctica, and South Africa. Few, if any, species are shared with extra-Gondwanan assemblages. The representation of plant groups, together with wood growth indices, palaeomagnetic data, and oxygen isotope signatures, suggests that the Western Australian marginal basins experienced humid seasonal mesothermal climates in mid-latitudes during the Neocomian–Barremian. Local variations between assemblages are probably attributable to differences in depositional settings, seasonal effects, and taphonomic factors rather than significant climatic or stratigraphic anomalies between localities and host formations.

ACKNOWLEDGEMENTS

Thanks are due to the numerous museum and university officers and members of the public who, over the past three decades, have contributed Cretaceous plant fossils from various localities to the Western Australian Museum and the University of Western Australia. Dr Ken McNamara and Dr John Long of the Western Australian Museum are thanked for arranging the loan of the museum's specimens. Dr David Haig (University of Western Australia) and Mr Glynn Ellis (University of Lausanne) assisted with

collecting in the Carnarvon Basin. This research was carried out while the author held an Australian Research Council Postdoctoral Fellowship at the University of Western Australia.

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Copepods from ground waters of Western Australia, I. The genera *Metacyclops*, *Mesocyclops*, *Microcyclops* and *Apocyclops* (Crustacea: Copepoda: Cyclopidae)

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Abstract – *Metacyclops mortoni* sp. nov. and *Mesocyclops brooksi* sp. nov. are described from ground waters of the Cape Range karst area, northwestern Australia. New localities for the species *Microcyclops varicans* G. O. Sars, 1863 and *Apocyclops dengizicus* (Lepechkin, 1900) are reported from the same area. The distribution of the above species is greatly extended to northwestern Australia.

INTRODUCTION

Until recently, notwithstanding the great extent and diverse geological, climatic and hydrological conditions of the Australian continent, very few studies were devoted to the taxonomy of copepods, especially of groundwater-inhabiting species. Even less is known of the copepod fauna of Australia outside Victoria, New South Wales and the Northern Territory.

The apparent scarcity of copepods in Australia probably results from a lack of collections over much of the continent, particularly from subterranean biotopes.

The number of recent publications on Australian freshwater copepods, especially groundwater species (Dumont and Maas 1985; Morton 1985, 1990; Hamond 1987; Dussart and Fernando 1988; Timms and Morton 1988; Pesce *et al.* 1996), reflect the growing recognition world wide of the extent and importance of groundwater communities (Marmonier *et al.* 1993). Nevertheless, the freshwater cyclopoid copepods, particularly those from northwestern Australia, remain almost completely unknown. Therefore, it is not surprising that collections from different subterranean habitats in this region included two hitherto undescribed species of the genera *Metacyclops* Kiefer and *Mesocyclops* G. O. Sars, and the widespread species *Microcyclops varicans* (G. O. Sars, 1863) and *Apocyclops dengizicus* (Lepechkin, 1900).

The discovery of *Metacyclops mortoni* sp. nov. increases to two the number of congeners from Australia, the others being *M. arnaudi* (G.O. Sars, 1908) and the subspecies *M. arnaudi platypus* Kiefer, 1967.

The genus *Mesocyclops* is better represented in Australia and, besides the new species, includes at

least five species viz. *M. notius* Kiefer, 1981, from Queensland and the Northern Territory, *M. darwini* Dussart and Fernando, 1988, from the Northern Territory, *M. australiensis* (= *M. thermocyclopoides australiensis*) (G. O. Sars, 1908), from New South Wales, Victoria and Tasmania, *M. cuttcuttae* Dumont and Maas, 1985, from the Northern Territory and *M. thermocyclopoides* Harada, 1931, from New South Wales and Victoria (Defaye and Kawabata 1993). *M. pehpeiensis* Hu, 1943, was recorded by Lim and Fernando (1985), but without locality data.

Finally, this paper considerably extends to the west the known distribution of both *M. varicans* and *A. dengizicus*, which were previously known within Australia only from New South Wales, Victoria and Northern Territory.

HABITAT AND ASSOCIATED FAUNA

Northwestern Australia is arid and on the Cape Range peninsula the available water is mostly groundwater accessible in a few caves within the Cape Range karst and in the general water table of the surrounding coastal plain where a freshwater lens overlies salt water (Humphreys 1993a, 1993c; 1993d). The area has a rich stygofauna with tethyan affinities (Humphreys 1993b, 1994; Humphreys and Adams 1991; Knott 1993).

Metacyclops mortoni was found only in hand-dug wells on the coastal plain of the Cape Range peninsula (C-25, C-149, C-273 and Waroora Well) and on the Ashburton River (Geebera Well) in water ranging in temperatures between 19.6 and 28.2°C and salinity between 2,550 and 17,044 mg L⁻¹. It was associated with an aquatic fauna that included Turbellaria, harpacticoid and calanoid

copepods, melitid amphipods (undescribed genus; W. D. Williams, pers. comm.), *Halosbaena tulki* Poore and Humphreys (Thermosbenacea), *Stygiocaris lancifera* Holthuis (Decapoda: Natantia), Hydracarina (Acarina), *Milyeringa veritas* Whitely (Perciformes: Eleotridae) and *Ophisternon candidum* (Mees) (Synbranchiformes: Synbranchidae).

Mesocyclops brooksi is known only from the type locality, Bobs Well, a hand-dug well in the Ashburton River valley, a river now remote from Cape Range but which formerly flowed past the tip of the peninsula (Wyrwoll *et al.* 1993). The water temperature was 25.0°C and the salinity was 1121 mg L⁻¹.

Apocyclops dengizicus was found only in a small piezometric tube located in a recently dug test pit in a back dune area adjacent to the ocean. The water temperature was 26.9°C and the salinity was 22,000 mg L⁻¹.

Microcyclops varicans was collected in a variety of habitats containing waters ranging in temperatures between 23.9 and 26.9°C and salinity between 99 and 9448 mg L⁻¹. These sites included a bore and a hand-dug well at the base of the Cape Range peninsula, a hand-dug well on the Ashburton River and, interestingly, water in the dark zone of an 80 m deep cave (C-18) within central Cape Range—where it occurs with a second species of the undescribed genus of melitid amphipod mentioned above, the only other aquatic species known from the range. This cave contains a diverse troglobitic fauna derived from a rain forest (both temperate and tropical) litter fauna – the area is now arid (Humphreys 1993a, 1993c). In addition, the aquatic insect *Copelatus irregularis* MacL. (Coleoptera: Dytiscidae) has been recorded in this cave (itself a big range extension from the Kimberley, central Australian Ranges and North-east Queensland).

MATERIAL AND METHODS

Groundwater was sampled for fauna at 261 sites on the Cape Range peninsula and in the Ashburton River valley in 1993; 185 of these sites yielded stygofauna (Figure 29). The groundwater was accessed through bores, wells, soaks, piezometers and caves. Bores were sampled for fauna using a plankton net with a 125 µm mesh and of a size suitable for the bore, the nets ranged from 30 mm to 180 mm in diameter. Wells were sampled by hand nets (125 µm mesh) and by Cvetkov (1968) phreatobiological nets (300 mm diameter, 250 µm mesh). Samples were variously taken through the entire water column and from various depths within the water column – occasionally the outflow from bore pumps was sampled by straining through a net (125 µm mesh). In all situations baited traps were sometimes used.

Comprehensive water analyses are available for

seven of the eleven sites mentioned in this paper (Humphreys 1994). Where direct measurements were not made the salinity (total soluble salt: TSS) was estimated from the electrical conductivity measured in the field.

Permanent mounts were made in commercial polyvinyl-lactophenol medium. Dissected specimens were drawn at magnification of 400x and 1000x, the latter using an oil immersion lens and "camera lucida" mounted on a Leitz Laborlux D phase-contrast microscope. Type material is deposited in the Western Australian Museum (WAM).

Terminology applied to body and appendages according to Huys and Boxshall (1991).

SYSTEMATICS

Family Cyclopidae Burmeister, 1834

Genus *Metacyclops* Kiefer, 1927; sensu Lindberg, 1961

Metacyclops mortoni sp. nov.
(Figures 1–15)

Material Examined

Holotype

♀ (WAM 183–94), Kudamurra Well (C–25), Cape Range peninsula, Western Australia (station BES 2199), Australia, 21°54'S, 113°49'E, 1 June 1993, R.D. Brooks.

Paratypes

Australia: Western Australia: 1 ♂ (allotype) (WAM 2–184), 2 ♀ (WAM 185, 186–94), Geebera Well, Ashburton River (BES 2321), 22°06'S, 115°08'E, 26 June 1993, R.D. Brooks and W.F. Humphreys; 2 ♀, (WAM 187, 188–94), Five Mile Well (C-273) (BES 2196), 21°51'S, 113°52'E, 1 June 1993, R.D. Brooks; 2 ♀ (WAM 189, 190–94), Tulki Well (C–149) (BES 2213), 22°05'S, 113°54'E, 2 June 1993, R.D. Brooks; 2 ♀ (WAM 191, 192–94), Waroora Well, Pt. Maud (BES 2227), 23°09'S, 113°48'E, 11 June 1993, R.D. Brooks.

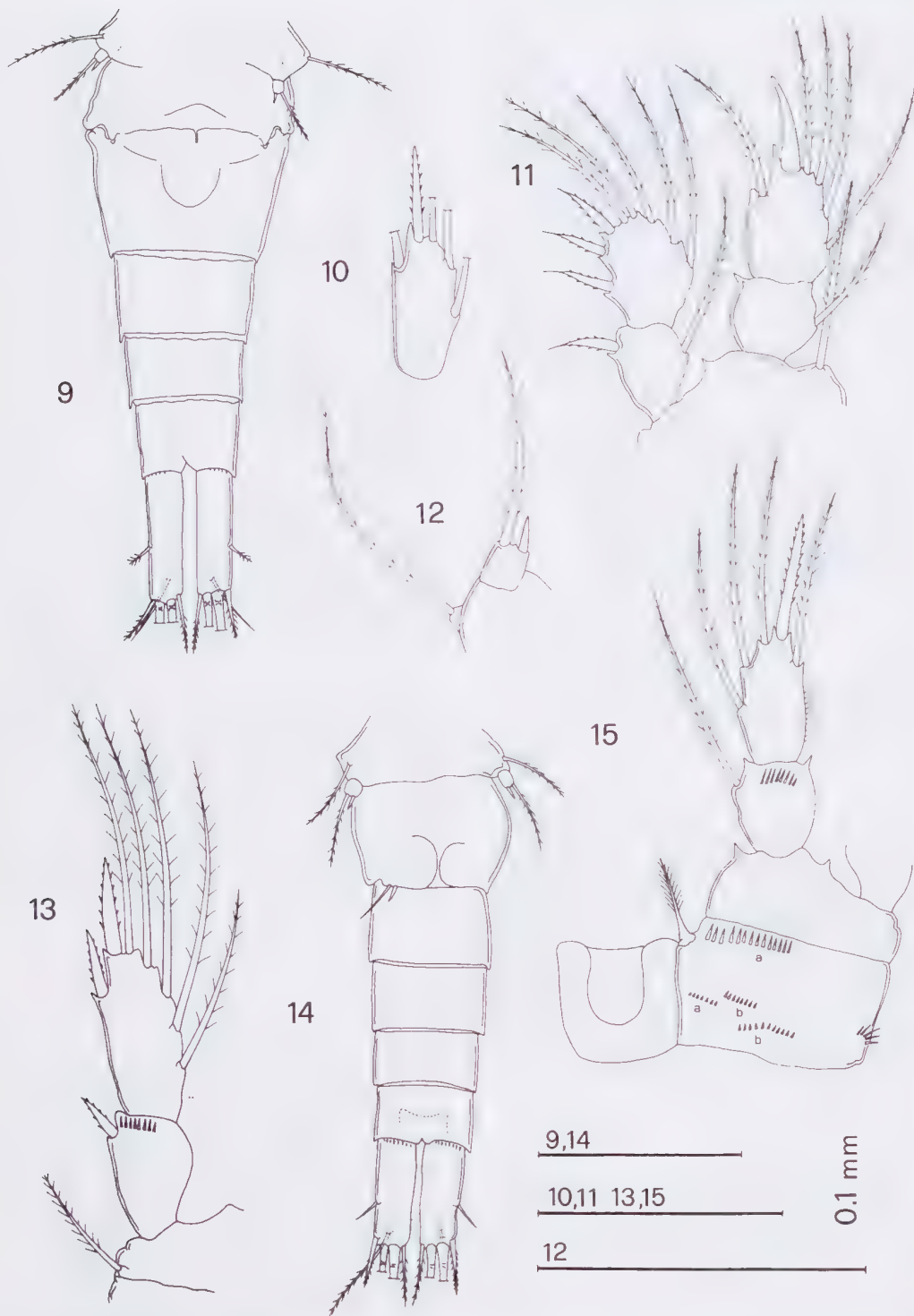
Description

Female

Length of holotype, excluding antennule and caudal setae, 555 µm; range of length of 6 paratypes 540–560 µm. Body widest at first prosomite. Genital segment about as long as broad, anterior 2/3 faintly expanded laterally; seminal receptacle with well developed subcircular anterior expansion, lateral canals almost horizontal. First urosomites naked, anal somite with small spinules along posterior margin; anal operculum not well defined.



Figures 1-8 *Metacyclops mortoni* sp. nov., 1-3, 5-8 (holotype), 4 (allotype): 1, mandible; 2, ♀ antennule; 3, basal segment of antennule, ventral; 4, ♂ antennule; 5, antenna; 6, maxilliped, posterior side; 7, maxilla; 8, maxillula.



Figures 9–15 *Metacyclops mortoni* sp. nov., 9, 11–13, 15 (holotype), 14 (allotype), 10 (female paratype): 9, urosome and caudal rami, ventral; 10, endopodite 3 of leg 4; 11, leg 1; 12, leg 5; 13, exopodite of leg 4; 14, urosome and caudal rami, ventral; 15, endopodite, basis, coxa and connecting plate of leg 4 (a: frontal side; b: caudal side).

Caudal rami, 3.6 (holotype), 3.5–3.7 (6 paratypes) times longer than broad; lateral seta inserted at distal half of ramus; dorsal seta shorter than ramus; terminal inner seta slightly longer than outermost.

Antennule 11-segmented, shorter than first prosomite; basipodite armed with 9 rows of small spinules, three dorsal, well-developed plumose setae and 7–8 lateral setae; remaining setation as in Figure 2.

Antenna 4-segmented; basipodite with well developed exopodal seta reaching about tip of the second segment, and one inner, subdistal plumose seta [type 3a, according to Reid (1991)]; first segment with one seta, second segment with eight setae, terminal segment with seven setae; no spine pattern was observed on both frontal and caudal side of the basipodite.

Maxilliped 4-segmented, comprising syncoxa, basis and 2-segmented endopodite; syncoxa armed with 3 inner plumose setae representing vestigial endites and a row of small spinules; basis with two inner plumose setae and numerous long spinules; first endopodal segment bearing a single spinulose seta and a row of 5–6 spinules, second endopodal segment with a spinulose seta and two shorter naked setae.

Mandible, maxillule and maxilla without particular characteristics as compared to those of congeners.

Swimming legs 1–4 with 2-segmented rami. Spine and setae formula of distal segments of exopodites 3.4.4.2 and 5.5.5.5, respectively. Couplers of all legs lacking ornament. Spine on the basipodite of leg 1 well developed, reaching about tip of distal segment of endopodite.

Leg 4, coxa with four rows of spinules, arranged as in Figure 15; distal segment of the endopodite about 2 times longer than broad, armed with one apical spine, slightly longer or about as long as the segment.

Leg 5 consisting of one free segment, slightly longer than broad; spine slightly shorter than segment.

Male (Allotype)

Length 530 μm . Habitus slender. Antennule geniculate, 17-segmented. Leg 5 similar to that of female. Leg 6 consisting of two spiniform setae, ventral seta shorter and stouter than dorsal one. Caudal rami sexually dimorphic, shorter ($L/I = 2.9\text{--}3.1$) than those of female.

Affinities

The genus *Metacyclops* (sensu Lindberg 1961) is widespread in tropical and temperate regions. At present it includes 52 named species and subspecies, only two, *M. arnaudi* and *M. arnaudi platypus*, are recorded from Australia.

Lindberg (1961) established two species-groups within the genus, viz. the minutus-group and the gracilis-group, embracing species characterized by one or two distal spines on the endopodite 3 of leg 4, respectively. *M. murtoni* is a member of the minutus-group, but it does not match any species in either Lindberg's (1961) or Herbst's (1988, 1990) keys of *Metacyclops*, because of the combination of the following characters: antennula 11-segmented, with first segment spinulose; basipodite of the antenna with 2 setae; legs 1–4 spine formula 3.4.4.2, endopodite 3 of leg 4 with one apical spine; couplers of legs 1–4 lacking ornament; inner caudal seta longer than outermost, male leg 6 consisting of 2 setae.

The spine formula 3.4.4.2 of legs 1–4 is a striking feature of the new species; within the genus *Metacyclops* deviation from the characteristic formula 3.4.4.3 has been reported only in *M. trispinosus* Dumont, 1981, from West Africa, which has a spine formula 3.3.3.3.

Etymology

The species is dedicated to Mr D.W. Morton in recognition of his recent valuable contributions to the knowledge of Australian copepods.

Genus *Mesocyclops* G. O. Sars, 1914

Mesocyclops brooksi sp. nov.

Figures 16–28

Material Examined

Holotype

♀ (WAM 193–94), Bobs Well, Ashburton River, Western Australia, Australia (BES 2333), 22°29'S, 115°23'E, 28 June 1993, W.F. Humphreys and R.D. Brooks.

Paratypes

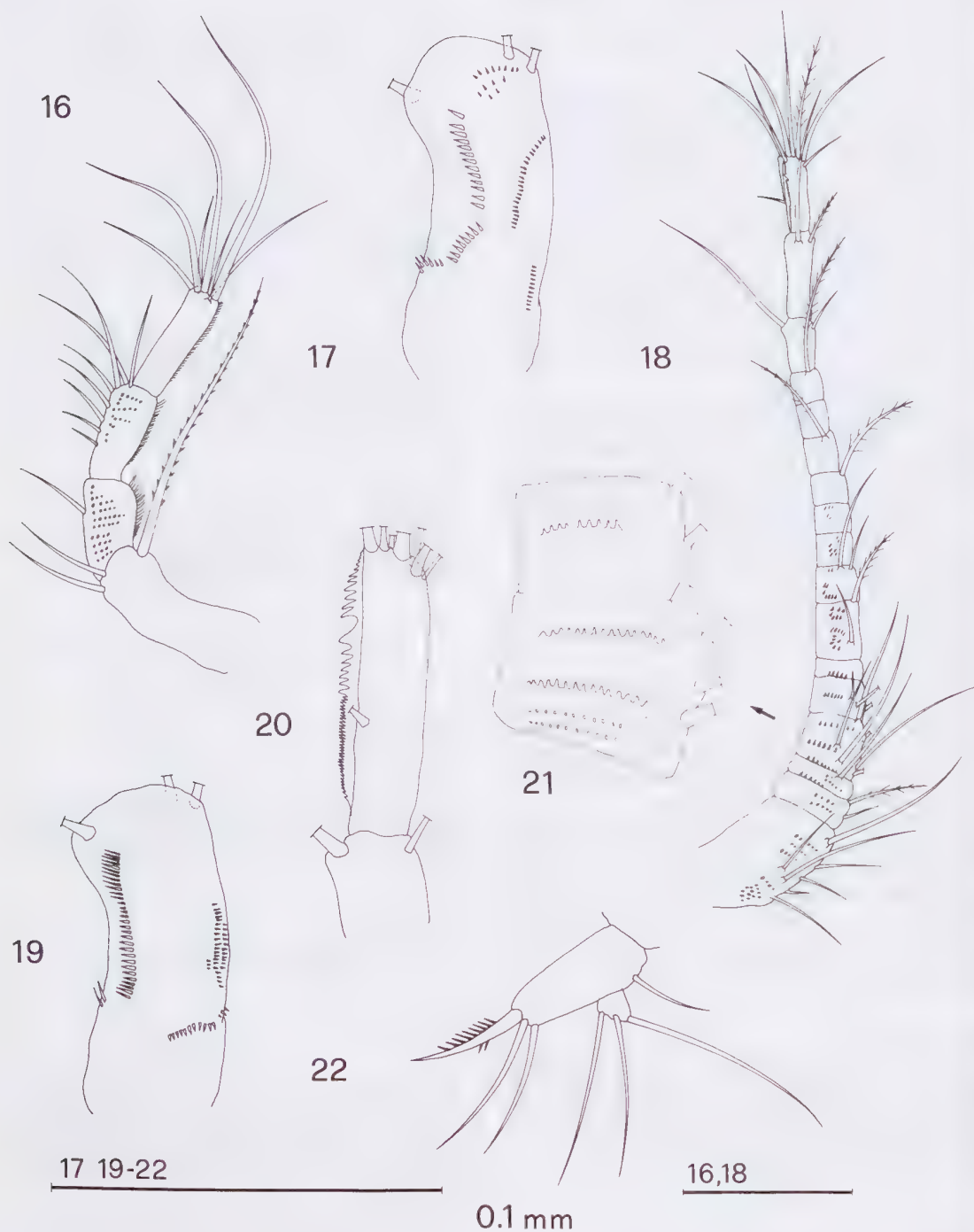
Australia: Western Australia: 1 ♀, 1 ♂, same data as holotype (WAM 194, 195–94).

Description

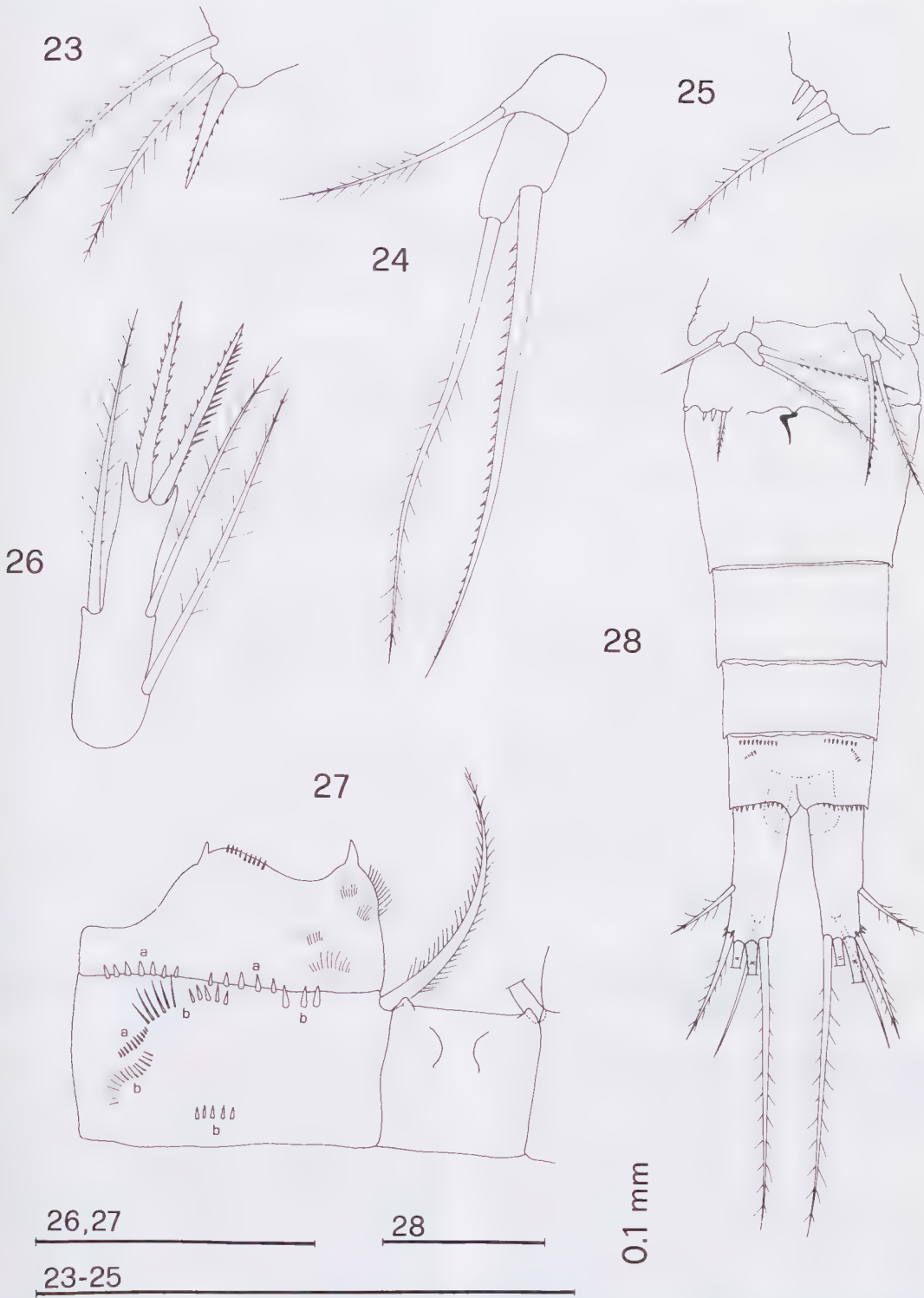
Female

Total body length 1350 μm (holotype), 1320 μm (paratype). Fifth thoracic segment with few setules laterally. Genital segment about as long as broad. Owing to the preparation the seminal receptacle is partially obscured in both specimens, pore canal recurved.

Antennule 17-segmented, reaching the distal margin of the third thoracic segment; spinule patterns are present on segments II–X; segments IV–V with two (IV) or one (V) crenelate lamellas; segments I–IV with several rows or groups of small integumental circular pits on dorsal surface; distal



Figures 16–22 *Mesocyclops brooksi* sp. nov. (holotype): 16, antenna; 17, antenna, basipodite (caudal side); 18, antennule; 19, antenna, basipodite (frontal side); 20, antennule, distal segment; 21, antennule, segment 4; 22, maxillulary palp.



Figures 23–28 *Mesocyclops brooksi* sp. nov., 23 (male paratype), 24–28 (holotype): 23, ♂ leg 6; 24, leg 5; 25, ♀ leg 6; 26, endopodite 3 of leg 4; 27, basis, coxa and connecting plate of leg 4 (a: frontal side; b: caudal side); 28, urosome and caudal rami.

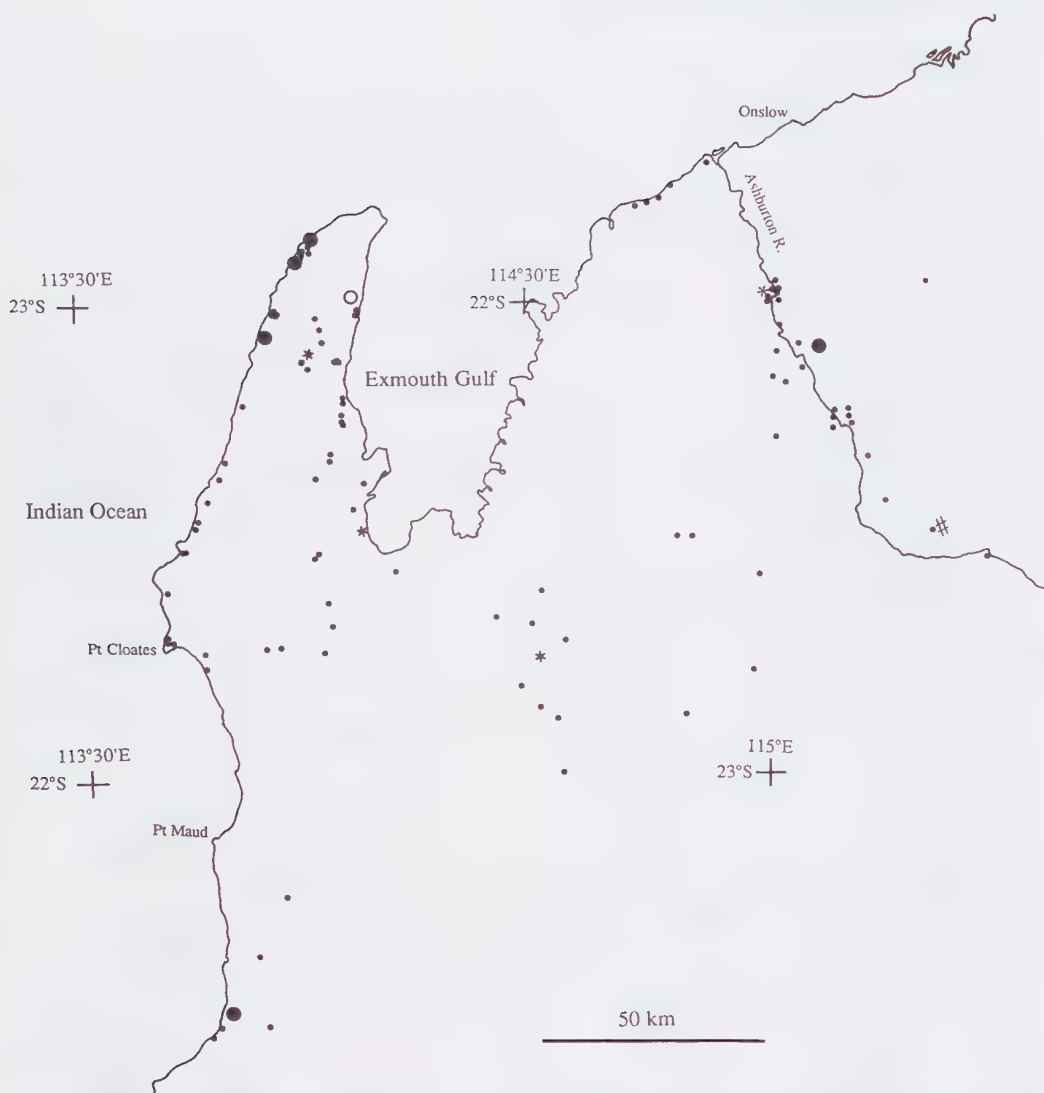


Figure 29 The location of the samples in northwestern Australia: *Metacyclops mortoni* sp. nov. (●); *Mesocyclops brooksi* sp. nov. (#); *Apocyclops dengizicus* (○); *Microcylops varicans* (*). The small dots denote sites where stygofauna was found.

segment with hyaline lamella provided with one deep notch; remaining ornamentation as in Figures 18, 20, 21.

Antenna. Endopodite 3-segmented; first segment with one inner seta, second segment with eight setae, third segment with an apical group of seven setae; segments I–II with rows of small integumental pits. All segments with a row of setules on the external side. Basipodite with vestigial exopodal seta overreaching tip of the distal segment of the endopodite, and two short subdistal setae, frontal side with the characteristic row of long spinules along the outer margin, 2–3 rows of small spinules on the inner margin, and a

transverse row of spinules below.

Maxillulary palp not provided with spines. Other mouthparts as usual in the genus.

Legs 1–4, spine and setae formula typical for the genus; couplers without setules on the caudal side. Leg 1, inner margin of the basipodite not armed with a spine. Leg 4: endopodite about 3.5 times longer than broad; apical spines subequal, outer spine equally serrated on both margins, inner spine with outer margin completely set with spinules, internal margin regularly serrated; couplers with pair of blunt tubercles, coxopodite armed with 3 (frontal side) and 4 (caudal side) rows of spines/setules; caudal side of the basipodite on its distal

internal margin with a row of small spinules, on its distal and subdistal margin with 4–5 rows of thin setules.

Leg 5. Spinous seta about as long as the plumose seta; setae not reaching to the posterior margin of the genital segment.

Leg 6 consisting of two small spines and one long plumose seta; characteristic group of small pores present at its basis.

Caudal rami about 3 times longer than broad, without cilia on the inner margins; dorsal seta longer than the apical outer seta, inner seta about 2.5 times longer than corresponding outermost.

Male

Smaller than females, total body length, excluding antennule and caudal setae, 1270 μm . Antennule geniculate, with integumental pits as in females. Spine and pit pattern on the basipodite and endopodite of antenna, structure of legs 1–5 and ornamentation of fifth thoracic segment as in females. Leg 6 consisting of a protuberance bearing one stout spine and two plumose setae.

Affinities

Mesocyclops is a cosmopolitan and widespread genus found mainly in surface fresh waters, rarely in ground waters. It includes 66 species and subspecies, which are especially common in the tropics and subtropics, a few species also occur in temperate and arctic regions.

Taxonomic understanding of the genus has greatly improved during recent years on account of recognition of formerly overlooked micro-characters, such as morphology of the hyaline lamella on the distal segment of the antennula, the presence or absence of spine patterns on the antennular segments, the presence or absence of spines on the maxillulary palp, the armature of the intercoxal plate of leg 4, the ornamentation of the spines on the distal segment of the endopodite of leg 4 and the presence or absence of setules on the fifth thoracic segments (Van de Velde 1984; Dussart and Fernando 1988; Reid 1993).

Following Kiefer's (1981) excellent review of *Mesocyclops*, the closest relatives to *M. brooksi* are *M. notius* and *M. australiensis*.

From the above species, *M. brooksi* is readily distinguishable by the shortness of the genital segment, the different length ratio between inner and outer distal spines on the endopodite 3 of leg 4 (subequal in *M. brooksi*, the inner shorter than outer in both *M. australiensis* and *M. notius*), the different serration along the margins of the inner apical spine of the endopodite of leg 4, and the shorter caudal rami.

Additionally, a salient feature of the new species is the integumental pits on the dorsal surface of the antennule and antenna, both in male and females.

Circular pits on some segments of the antennule in *Mesocyclops* species were firstly pointed out by Von Daday (1906), who interpreted them as integumental tubercles. Subsequently, Reid and Saunders (1986) reported similar structures in specimens of *Mesocyclops aspericornis* (Von Daday, 1906) from Venezuela, considering them as sensory structures, advantageous in spatially restricted habitats. Nishida (1986) showed identical structures in marine cyclopoids of the genus *Oithona*, interpreting them as chemo- or mechanoreceptors in mating behaviour, which could represent "areas of increased friction during copulation". Reid and Saunders (1986) also referred to such integumental pits in species of the genus *Thermocyclops*, suggesting that closer investigations of these structures should be carried out in future species descriptions.

Etymology

Named after Mr R.D. Brooks, a collector of the new species.

Genus *Microcyclops* Claus, 1893

Microcyclops varicans (G. O. Sars, 1863)

Material Examined

Australia: Western Australia: 2 ♀ (WAM 196, 197–94), Cashen Well, Exmouth Gulf Station (BES 2146), 22°29'S, 114°06'E, 24 May 1993, W.F. Humphreys and R.D. Brooks; 1 ♀ (WAM 198–94), River Well, Ashburton River (BES 2318), 22°00'S, 115°02'E, 26 June 1993, W.F. Humphreys and R.D. Brooks; 1 ♀ (WAM 199–94), Dry Swallet Cave (C-18), Cape Range (BES 2372), 22°05'S, 114°00'E, 12 July 1993, R.D. Brooks; 1 ♀ (WAM 200–94), Number 8 Bore, Cape Range peninsula (BES 2379), 22°45'S, 114°31'E, 20 July 1993, R.D. Brooks.

Genus *Apocyclops* Lindberg, 1942

Apocyclops dengizicus (Lepechkin, 1900)

Material Examined

Australia: Western Australia: 1 ♀ (WAM 201–94), Marina piezometer bore C, Exmouth (BES 2234); 21°57'S, 114°08'E, 16 June 1993, R.D. Brooks.

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Copepods from ground waters of Western Australia, II. The genus *Halicyclops* (Crustacea: Copepoda: Cyclopidae)

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Abstract – *Halicyclops longifurcatus* n.sp. is described from groundwaters of the Cape Range karst area, north-western Australia. *Halicyclops spinifer* Kiefer 1935, from the same region, is for the first time recorded from Australia. These findings increase to three the number of congeners from Australia, the other being *H. ambiguus* Kiefer, 1967, reported from the southeastern part of the continent.

INTRODUCTION

Cyclopoid copepods have recently been collected from a variety of different groundwater habitats (sinkholes, anchialine caves, wells) on the Cape Range peninsula, northwestern Australia. The material included several interesting stygobitic and stygophilic species, amongst them an undescribed species of the genus *Halicyclops* Norman and the species *Halicyclops spinifer* Kiefer, 1935.

Halicyclops is a cosmopolitan genus, with 72 named species and subspecies, widely distributed in coastal brackish waters, ponds, marshes and sandy beaches; nineteen species, the new species included, are stygophilic inhabitants of ground water habitats, such as anchialine caves, sinkholes and different interstitial media.

The present finding increases to three the number of *Halicyclops* species from Australia, the other being *H. ambiguus* Kiefer, 1967, described from southeastern Australia.

Habitat and associated fauna

North-western Australia is arid and on the Cape Range peninsula the available water is mostly groundwater accessible in a few caves within the Cape Range karst as well as in the general water table of the surrounding foothills and coastal plain where a freshwater lens overlies salt water (Humphreys 1993a, 1993c, 1993d).

Halicyclops longifurcatus is known only from an anchialine flooded sinkhole (cenote), 1.6 km from the ocean (Figure 24). The specimens were collected by hauling a plankton net (125 µm mesh) through the water above the marked thermo-halocline which occurs at a depth of ca. 6 m. A number of taxa have been recorded from the sinkhole above the thermo-halocline: foraminiferida, *Iravadia* sp. (Mollusca: Irvadiidae), ostracods, *Stygocaris*

stylifera Holthuis (Malacostraca: Decapoda: Natantia: Atyidae), gerrids (Hemiptera), chironomids (Diptera), *Milyeringa veritas* Whitely (Perciformes: Eleotridae) and the algae *Rhizoclonium ?tortuosum* (Dillw.) Kuetz. (Chlorophyta: Cladophoraceae) and *Lamprothamnium papulosum* (Wallr.) J. Gr. (Charophyta: Characeae). Below the halocline occurs a strictly anchialine fauna (Yager and Humphreys 1996) with tethyan affinities (Humphreys 1993b; Humphreys and Feinberg 1994; Knott 1993). This fauna includes *Lasioneustes exleyi* (Remepedia: Speleonectidae- Yager and Humphreys 1996), *Liagoceradocus* sp. nov. (Amphipoda: Hadziidae- Bradbury and Williams 1995) and *Danielopolina* sp. nov. (Ostracoda: Thaumatoctypriidae – Baltanas and Danielopol 1995).

At the surface the salinity was 20,000 mg L⁻¹ and below the thermo-halocline the salinity gradually increased with depth to 32,000 mg L⁻¹. The surface temperature was 28.5°C and dropped to 25.0°C at the thermocline, increasing with depth to 26.3°C.

Halicyclops spinifer occurred in a hand-dug pastoral well (C-361) near the coast with a salinity of 1,400 mg L⁻¹, and at 200 m above sea level in a deep cave (C-18) in central Cape Range where the salinity was 500 mg L⁻¹. The fauna associated with C-361, but not at the time of sampling for *H. spinifer* includes *Milyeringa veritas* and *Ophisternon candidum* (Mees) (Synbranchiformes: Synbranchidae), *Stygocaris stylifera*, dipteran larvae and harpacticoid copepods. The water in C-18 contains *Microcyclops varicans* (Copepoda: Cyclopidae) (Pesce *et al.* 1996), a melitid amphipod (undescribed genus: W. D. Williams, per. comm.), and the aquatic insect *Copelatus irregularis* MacI. (Coleoptera: Dytiscidae) (further details in Pesce *et al.*, 1996).

MATERIAL AND METHODS

Various plankton nets (mesh size 125 μm) were used to collect copepods from wells, bores, caves and anchialine pools on the Cape Range peninsula and its hinterland in northwestern Australia, as described fully in Pesce *et al.* (1996).

Specimens, completely dissected, were mounted on cover slips in commercial polyvinyl-lactophenol. The figures were prepared using a camera lucida on a Leitz Laborlux D phase-contrast microscope.

Holotype and paratypes of the new species, and material of *H. spinifer*, are deposited in the Western Australian Museum, Perth, Australia (WAM); one paratype was deposited in the Museo Civico di Storia Naturale, Verona (Italy).

Terminology applied to body and appendages according to Huys and Boxshall (1991).

Family Cyclopidae Burmeister, 1834

Subfamily Halicyclopinæ Kiefer, 1927

Genus *Halicyclops* Norman, 1903

Halicyclops longifurcatus sp. nov.

Figures 1–11, 24

Material Examined

Holotype

♀ (WAM 248–94), Bundera Sinkhole (karst index number C-28), (BES 2470), Cape Range Peninsula, Western Australia, Australia, 22°25'S, 113°46'E, 6 August 1993, W.F. Humphreys and R.D. Brooks.

Paratypes

Australia: Western Australia: 9 ♀, 1 juvenile (WAM 249–94 to 257–94 and 263–94), same data as holotype; 1 ♀ (BES 2476: WAM 258–94), same locality as BES 2470.

Description

Female (holotype)

Body length 755 μm , body length range of 11 paratypes 750–760 μm . Hyaline fringes of prosomites smooth. Genital double somite about as long as broad, expanded into two rounded lateral protuberances. Hyaline fringes of genital double somite and subsequent somites serrate, fourth urosomite with small denticles on the dorsal side of hyaline fringe.

Caudal ramus long, 4.6 (holotype), 4.5–4.7 (paratypes) times longer than broad; inner apical seta reduced to slender and naked seta, outermost apical seta about as long as lateral seta; dorsal seta as long as ramus; inner middle apical seta bearing 4–5 spinules on distal part of basal half, terminal half irregularly plumose, outer middle apical seta

with 5–6 spinules on distal half, irregularly plumose distally.

Antennule 6-segmented, armed as in Figure 3. Antenna 3-segmented; basis with two inner distal plumose setae and one outer exopodal seta; middle segment with one inner seta; distal segment with 5 inner and 7 apical setae (some plumose).

Mandible reduced to coxa and gnathopod; palp consisting of two setae inserted on small protuberance.

Maxillula: praecoxa bearing four setae and two spines on inner side and four stout spines distally; palp consisting of basis bearing three setae on inner margin, one proximal exopodal seta and endopodite with three distal setae.

Maxilla as in Figure 2. Maxilliped 2-segmented; proximal segment bearing two setae, terminal segment with two inner modified setae and three long apical setae.

Swimming legs 1–4 armament as follows (roman numerals denote spines, arabic numerals denote setae).

	coxa	basis	endopodite	exopodite
leg 1	0–1	1–I	0–1;0–1;II–4	I–1;I–1;III–5
leg 2	0–1	1–0	0–1;0–2;III–3	I–1;I–1;IV–5
leg 3	0–1	1–0	0–1;0–2;III–3	I–1;I–1;IV–5
leg 4	0–1	1–0	0–1;0–2;III–2	I–1;I–1;III–5

Leg 1, basis with spine at inner corner overreaching the posterior border of the endopodite segment 2. Legs 2–3 similar to each other; distal endopodite segment with proximal seta plumose basally and spinulose distally. Leg 4 endopodite segment 3 longer than broad (1.48–1.57:1); inner apical spine slightly longer than segment and about 2 times longer than outer apical spine; inner setae spiniform, about equal in length, but only the proximal one basally plumose.

Leg 5 exopodite about twice as longer as broad, and armed with one apical seta and three serrated spines.

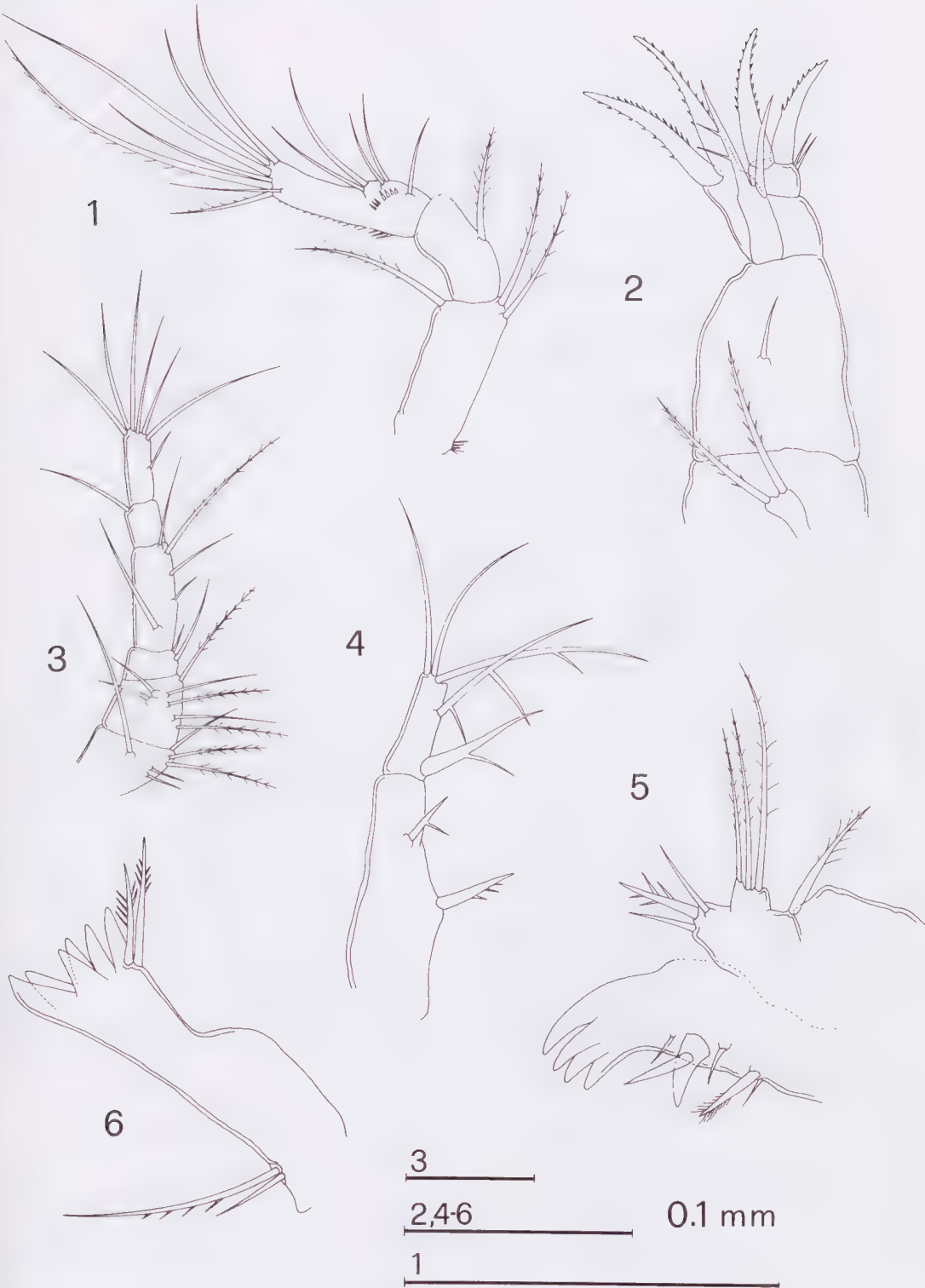
Male

Unknown.

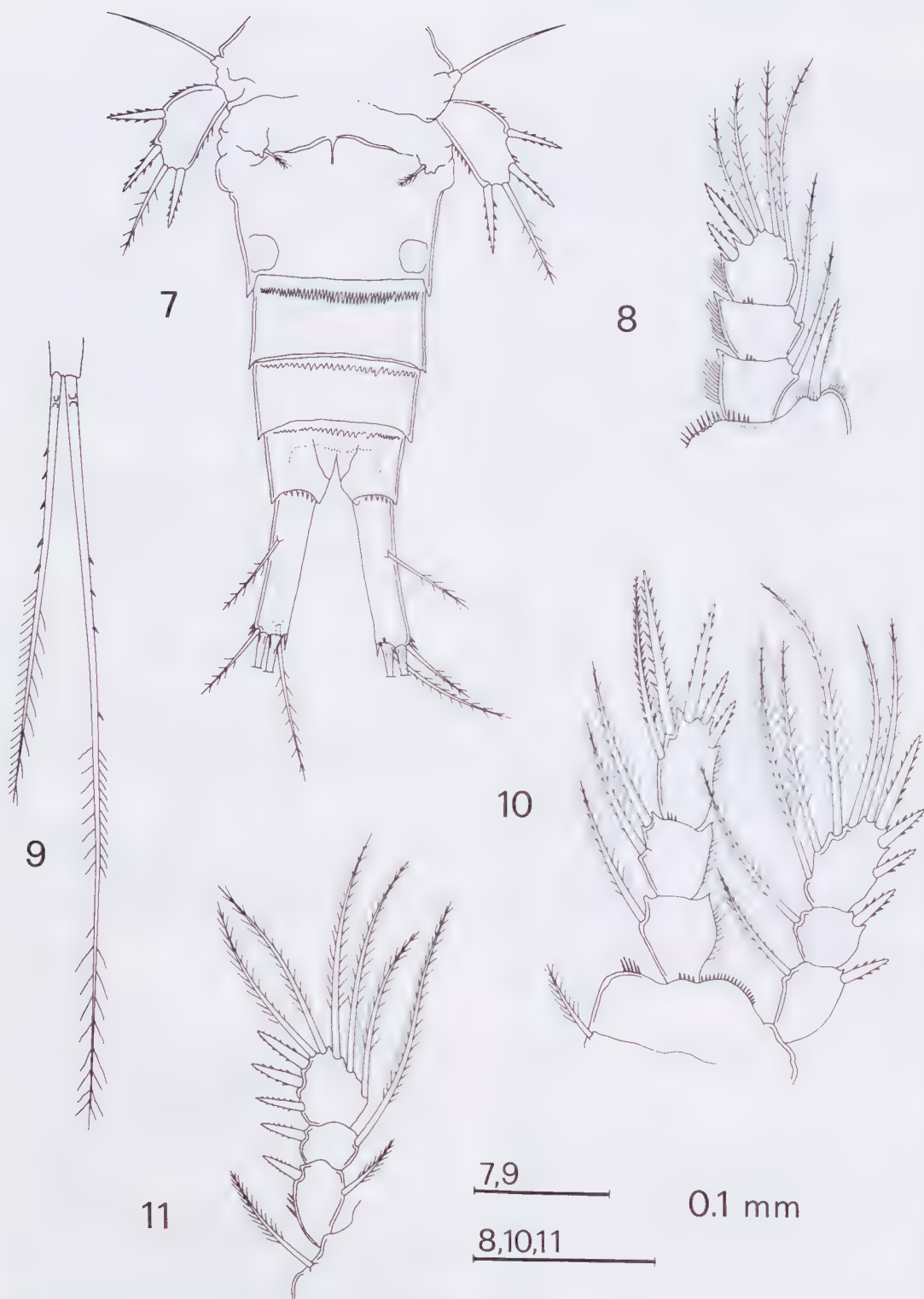
Differential Diagnosis

Several species of *Halicyclops* share with *H. longifurcatus* the lateral rounded protrusions on the genital double somite, the exopodite spine formula 3.4.4.3, and the poorly developed hyaline fringe on the fourth urosomite (Lindberg 1957).

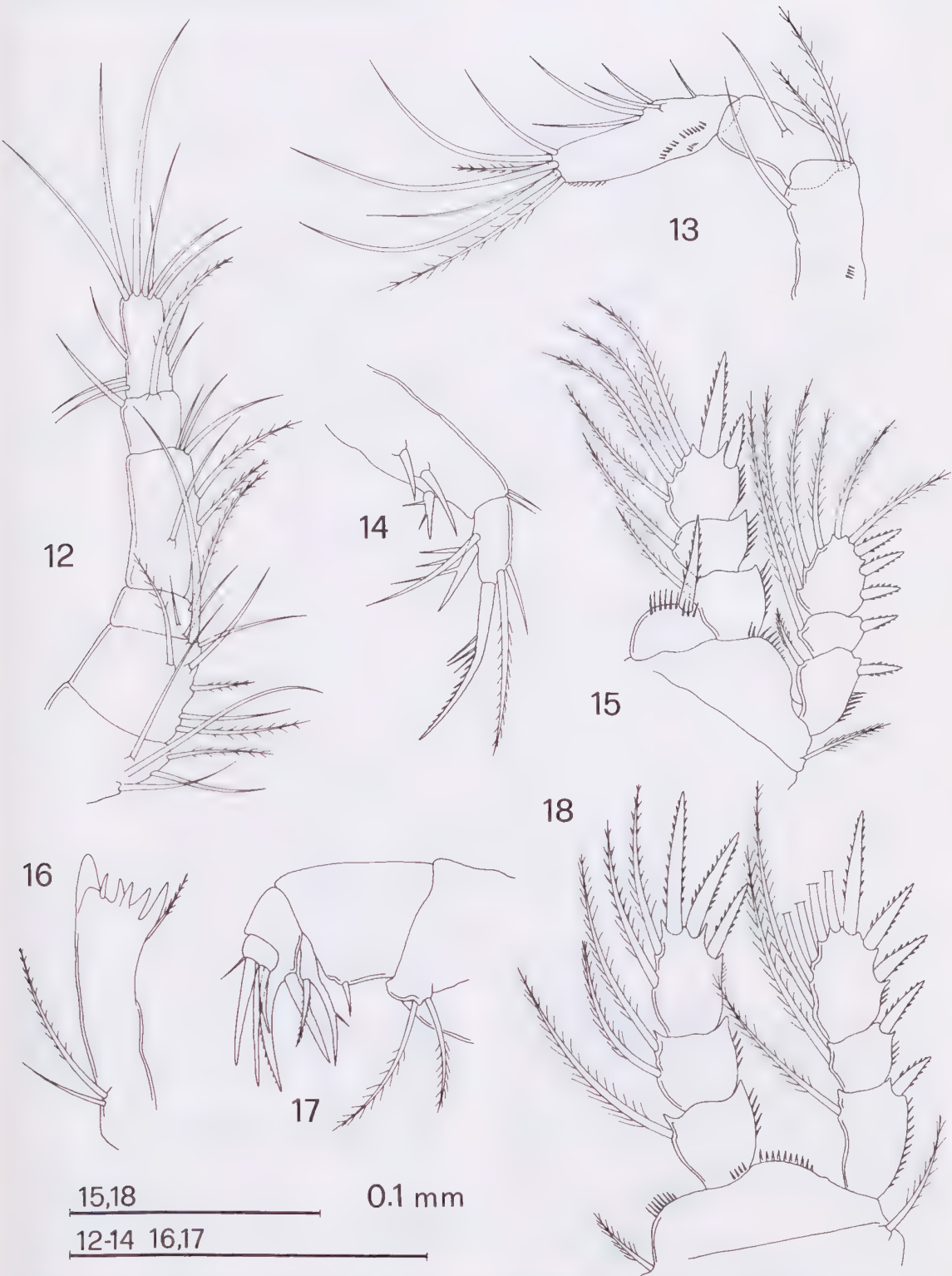
From these species, as well as from other congeners, the new species may be distinguished easily by the remarkable length of caudal rami, unusual for species of the genus *Halicyclops*, and by the mandibular palp bearing two setae.



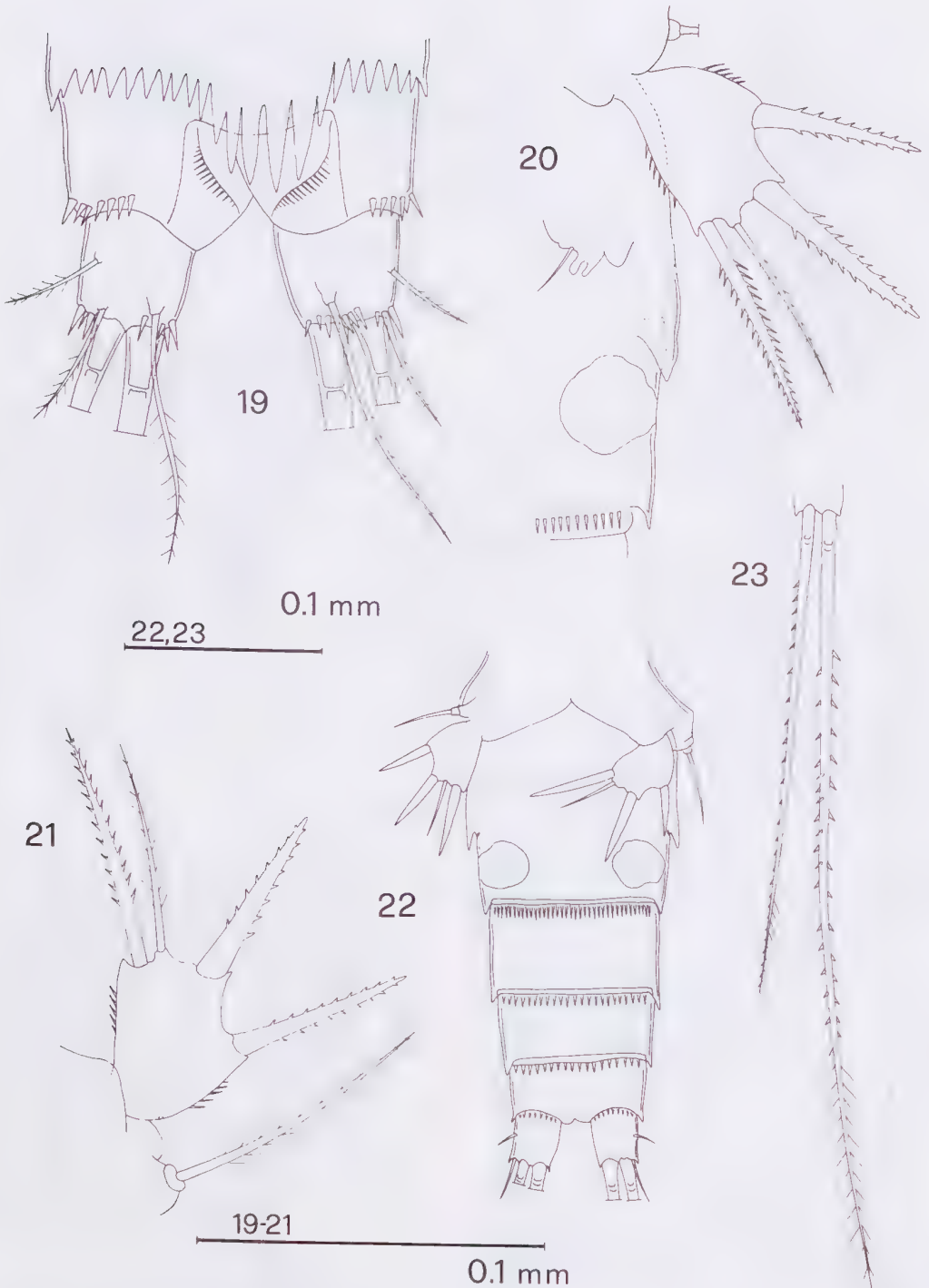
Figures 1-6 *Halicyclops longifurcatus* sp. nov. (holotype): 1, antenna; 2, maxilla, inner; 3, antennula; 4, maxilliped; 5, maxillula; 6, mandible.



Figures 7–11 *Halicyclops longifurcatus* sp. nov. (holotype): 7. abdomen and caudal rami, ventral view; 8. endopodite of leg 1; 9. middle apical caudal setae; 10. leg 4; 11. exopodite of leg 1.



Figures 12-18 *Halicyclops spinifer*: 12, antennula; 13, antenna; 14, maxilliped; 15, leg 1; 16, mandible; 17, maxilla; 18, leg 4.



Figures 19–23 *Halicyclops spinifer*: 19, anal somite and furcal rami, dorsal view; 20, legs 5–6, and lateral spine on genital somite; 21, leg 5; 22, abdomen and caudal rami, ventral view; 23, medial caudal setae.



Figure 24 Location of the collection sites for *Halicyclops longifurcatus* sp. nov. (○) and *H. spinifer* (□) in northwestern Australia. The small dots denote sites where stygofauna was found.

Etymology

The specific epithet is derived from the remarkable length of the caudal rami, unusual for the species of *Halicyclops*.

Halicyclops spinifer Kiefer, 1935

Figures 12–24

Material Examined

Australia: Western Australia: 2 ♀ and 1 juv. (WAM 260–94 to 262–94), Mowbowra Well (BES 2221), Cape Range peninsula, 22°00'S, 114°07'E, 9 June 1993, R.D. Brooks; 1 ♀ (WAM 259–94), cave C-18 (BES 2372), Cape Range peninsula, 22°05'S, 114°00'E, 12 July 1993, R.D. Brooks.

Supplementary Description

Body length, 540 µm (holotype), 550–560 µm (2 paratypes). Hyaline fringes of all prosomites smooth. Genital double somite slightly longer than broad, with a well developed chitinous, sharp spine curved backward on each side. Hyaline fringes of genital double somite and two subsequent somites serrate; hyaline fringe of urosomite 4 well developed dorsally, with dorsomedial denticulations much longer and stouter than lateral ones.

Caudal ramus about as long as broad; innermost apical seta difficult to distinguish from row of spinules along distal margin of ramus; outermost apical seta about as long or slightly longer than

ramus; dorsal seta about three times longer than ramus; inner middle apical seta bearing numerous spinules on both sides of basal and middle part, plumose distally; outer middle apical seta barbed on the inner distal margin, spinulose along the outer margin.

Antennule 6-segmented, armature as in Figure 12. Antenna 3-segmented; basis with two inner distal plumose setae and one outer subdistal exopodal seta, second segment with one inner seta, distal segment with 5 inner and 7 apical setae (some plumose).

Mandible, maxillule and maxilla without particular characteristics as compared to the original description.

Maxilliped 2-segmented; proximal segment with three inner spiniform setae (one modified) and two outer subdistal setules; distal segment bearing two inner modified setae and three apical and subapical setae.

Swimming legs 1-4 armature as follows (numerals as in *H. longifurcatus*):

	coxa	basis	endopodite	exopodite
leg 1	0-1	1-I	0-1;0-1;II-4	I-1;I-1;III-5
leg 2	0-1	1-0	0-1;0-2;III-3	I-1;I-1;IV-5
leg 3	0-1	1-0	0-1;0-2;III-3	I-1;I-1;IV-5
leg 4	0-1	1-0	0-1;0-2;III-2	I-1;I-1;III-5

Leg 1 basis with spine at inner corner reaching about the posterior border of the endopodite segment 2. Legs 2-3 similar to each other, distal endopodite segment with proximal seta plumose basally and serrate distally. Leg 4 endopodite segment 3 about 1.3 times longer than broad, inner apical spine longer than segment and outer apical spine; inner setae plumose basally and spinulose distally.

Leg 5 exopodite slightly longer than broad, and armed with one seta and three serrated spines, longer than segment.

Leg 6 as in Figure 20.

Remarks

H. spinifer fits a group of species [*thermophilus* group, according to Herbst (1983)] which are characterized by a well developed chitinous spiniform process on each side of the genital double somite.

The nominate group includes the following other species: *H. thermophilus* Kiefer, 1929; *H. venezuelaensis* Lindberg, 1954; *H. japonicus* Ito, 1956; *H. latus* Shen and Tai, 1964; *H. antiguaensis* Herbst, 1983; *H. dedeckeri* Brownell, 1983.

Comparison between the specimens from Australia and the original description of *H. spinifer*, revealed minor differences only in the shape of the genital double somite and pseudopericulum, and in the size of the lateral spines on the genital double

somite. For the latter, however, Falavigna da Rocha (in litt.) showed wide variation in the number and size of spinules forming the pseudopericulum, in the length/width ratio of the genital double somite, as well as in the shape and size of the lateral spines of the same somite in specimens of *H. spinifer* from Brazil.

From a biogeographical point of view, beside the Australian continent, *H. spinifer* is at present known for India, Iran and Brazil (Falavigna da Rocha, in litt.).

ACKNOWLEDGEMENTS

For determining the associated fauna we thank Mrs S. Slack-Smith, Dr T. Entwisle and Dr. L. B. Holthuis. We are also grateful to Dr J.W. Reid and Dr C. Plesá for valuable suggestions, and to Dr Falavigna da Rocha for reading and commenting on the manuscript. Field collecting was funded by the National Estate Grants Scheme and the water analysis by the Water Authority of Western Australia.

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Manuscript received 15 December 1994; accepted 12 March 1996.

A new species of *Samarangopus* (Myriapoda: Pauropoda) from
Papua New Guinea

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Abstract – The class Pauropoda has been identified for the first time from Papua New Guinea. The material belongs to a new species in *Samarangopus*, *S. papuensis* sp. nov., of the family Eurypauropodidae. The Australian species *Eurypauropus speciosus* Harrison is transferred to the genus *Samarangopus*.

INTRODUCTION

The pauropod fauna of Australasia and surrounding islands is relatively uninvestigated and very few papers have been published. A few haphazard finds have been made from Java (Silvestri 1930), Borneo (Scheller 1994), Mindanao, Peleliu among the Palau Islands and Guam (Remy 1957), resulting in 12 species, which is probably only a small fraction of the real fauna.

Thanks to Dr W. F. Humphreys, Western Australian Museum, we are now able to add a pauropod to the New Guinean fauna, which he collected from Baiteta near Madang in equatorial northern Papua New Guinea. This specimen is found to belong to a new species in the genus *Samarangopus* (Eurypauropodidae). That genus is known earlier from some adjacent areas: Java (Silvestri 1930), Borneo (Scheller 1994), New Caledonia (Remy 1956b, Scheller 1993) and probably also from New South Wales as Harrison (1914) briefly described *Eurypauropus speciosus* from Lobster Beach, Broken Bay. The latter species is here tentatively transferred to *Samarangopus*: *S. speciosus* (Harrison), **comb. nov.**

Provisional list of the species of the genus *Samarangopus*:

Species	Localities	References
<i>S. browni</i> Remy	New Caledonia	Remy 1956b
<i>S. doiinthanonaeus</i> Scheller	Thailand	Scheller 1995
<i>S. flabrarius</i> Remy	Madagascar	Remy 1956a
<i>S. jacobsoni</i> (Silvestri)	Java	Silvestri 1930
<i>S. molestus</i> Remy	Mauritius	Remy 1959
	Réunion	Remy 1959
<i>S. oxypygus</i> Remy and Rollet	Madagascar	Remy and Rollet 1960
<i>S. palearum</i> Scheller	New Caledonia	Scheller 1993
<i>S. papuensis</i> sp. nov.	Papua	
	New Guinea	This paper
<i>S. poculifer</i> Scheller	Thailand	Scheller 1995
<i>S. saproxylophilus</i> Remy	Madagascar	Remy 1956a
<i>S. segniter</i> Scheller	Borneo	Scheller 1994

<i>S. spathaceus</i> Scheller	New Caledonia	Scheller 1993
<i>S. speciosus</i> (Harrison)	Australia, New South Wales	Harrison 1914
<i>S. umbonifer</i> Scheller	Thailand	Scheller 1995
<i>S. umbraculus</i> Scheller	New Caledonia	Scheller 1993

In addition, Remy (1959) described *Samarangopus* sp. from Mauritius and Réunion.

Because the present author has studied several other species occurring in some collections from the Australasian region, the genus seems to be rich in species there. The above list probably enumerates a small fraction only of the species of the genus and therefore a useful key can not be constructed at present.

The abbreviations used below follow Hasenhütl (1986), and the sole specimen examined is lodged in the Western Australian Museum, Perth (WAM).

SYSTEMATICS

Family Eurypauropodidae Ryder

Subfamily Eurypauropodinae Verhoeff

Genus *Samarangopus* Verhoeff

Samarangopus Verhoeff, 1934: 189.

Diagnosis

An Eurypauropodinae genus with 5-segmented legs with one main claw and one anterior secondary claw; antennal globulus short-stalked and the anterior margin of the sternal antennal branch shorter than posterior one; anterior antennal flagellum F_2 shorter than posterior one F_3 .

Samarangopus papuensis sp. nov.
Figures 1–18

Type material

Holotype

Adult ♀, Baiteta, Madang Province, Papua New

Guinea, 5°00'37"S, 145°46'08"E, lowland rain forest, Tullgren funnel litter extraction, 9 May 1990, W. F. Humphreys (WAM 95/767, PNG 1990:833).

Description

Adult female (holotype)

Length. 0.65 mm.

Head. Head setae only partly distinguishable. Setae cylindrical, annulate. Vertex: not studied. Tempus: only one seta, $l \approx 10 \mu\text{m}$. Frons: no frontal pores; no pistil; ?frontal verruca. Index of frontal setae: median row, $mp = 16$; lateral row, four setae, $lp_1 = 13$, $lp_2 = 16$, $lp_3 = 10$, $lp_4 = 10$, $lp_2 - lp_3 = 6$, $lp_1 - lp_4 = 15$. Temporal organ: $l = 28 \mu\text{m}$.

Antennae (Figure 2). Cuticle of basal antennal segments and branches glabrous, segments three and four almost glabrous. Chaetotaxy of segments 1–4: 2/2/2 + $g'/3$. Setae cylindrical, annulate, segment 1, $p = 8$, $p' = 6$; segment 2, $p = p' = 9$; segment 3, $p = 8$, $p' = 10$, g' very small, spherical; segment 4, $p = 7$, $p' = 13$, $p'' = 9 \mu\text{m}$, the setae p''' , u and r absent. Sternal branch s , anterior margin = 10, posterior margin = 15, ϕ of base = 6.5, maximum $\phi = 8.5$, $q = 12 \mu\text{m}$. Anterior margin/length of $g = 1.1$; anterior margin/length of $q = 0.8$; anterior margin/posterior margin = 0.7; anterior margin/maximum $\phi = 1.2$; maximum ϕ/ϕ of base = 1.3. Globulus g , length = 9, $\phi = 6$, ϕ of base = 2 μm ; number of bracts ≈ 9 , their length = 5–6 μm ; capsule subspherical, $\phi = \pm 3.5 \mu\text{m}$. Tergal branch t fusiform, length = 16, ϕ of base = 5.5, maximum $\phi = 6 \mu\text{m}$; pore not identified; length of t /maximum $\phi = 2.7$. Relative lengths of flagella (base segments included): $F_1 = 68$ and 71 , $F_2 = 28$, $F_3 = 59$. Base segments glabrous, their lengths: $bs_1 = bs_2 = 11$, $bs_3 = 6 \mu\text{m}$. The F_1 4.3–4.4 times as long as t , F_2 and F_3 1.9 and 3.9 times as long as s respectively. Calyces helmet-shaped, those of F_1 large, those of F_2 and F_3 smaller.

Trunk. Setae of collum segment (Figure 3) similar in shape and length, furcate; primary branch subcylindrical, tapering, pointed, striate; secondary one short, tapering, pointed, glabrous; lengths of setae = 7 μm ; sternite process with short pubescence most anteriorly; appendages about as wide as long, glabrous, cap glabrous.

Tergite I with sublateral ridges which turn inwards anteriorly, tergites II–V with sublateral ridges, on VI two transverse ridges, a longer anterior one and a short posterior one (Figure 1). Tergites with three types of protuberances: (1) on anterior margin of tergite I, lateral margins of II–V and posterolateral margins of VI they are large wedge-shaped to campanulate with a distinct collar or they are reduced (Figures 4, 6, 8, 9, 12); (2) smaller fungiform ones with a disc-like round cap attached to a cylindrical but in distal part widened stalk (Figures 4–6, 8, 9, 12); (3) a great many more

or less evenly distributed small cones projecting outwards under the cuticle (Figures 4–9, 12). Tergite I with 27 protuberances of the first mentioned type at anterior and anterolateral margins and several fungiform protuberances inside the anterior and lateral margins and on the ridges (Figures 4–6); tergite II with wedge-shaped and campanulate protuberances at lateral margins, those nearest to pit of T_1 rudimentary (Figure 8); fungiform ones inside these rows and on the ridges; posterior margin with irregular blunt teeth (Figure 7); tergites III–VI similar to II (Figure 13). Tergite VI with only one campanulate seta at each inner margin of the pit of T_5 (Figure 12).

Number and lengths of lateral wedge-shaped or campanulate protuberances (format according to Scheller 1993): I, no. 27 (anterior and lateral), lengths = 10–17; II, no. 1 (very small) – $T_1 - 8 - 1$ (small), lengths = 2–20; III, no. 1 (small) – $4/5 - T_2 - 1$ (small) – 5 – 1 (small), lengths = 8–17; IV, no. 1 (very small) – 1 (small) – 4 – $T_3 - 1$ (small) – $4/5$, lengths = 9–18; V, no. 1 (small) – 5 – $T_4 - 1$ (small) – 3, lengths = 9–17; VI, no. 6 (increasing in length posteriorly) – $T_5 - 1$, lengths = 8–15 μm . Length/width ratio of tergites: I = 0.5, II = III = IV = VI = 0.4, V = 0.5.

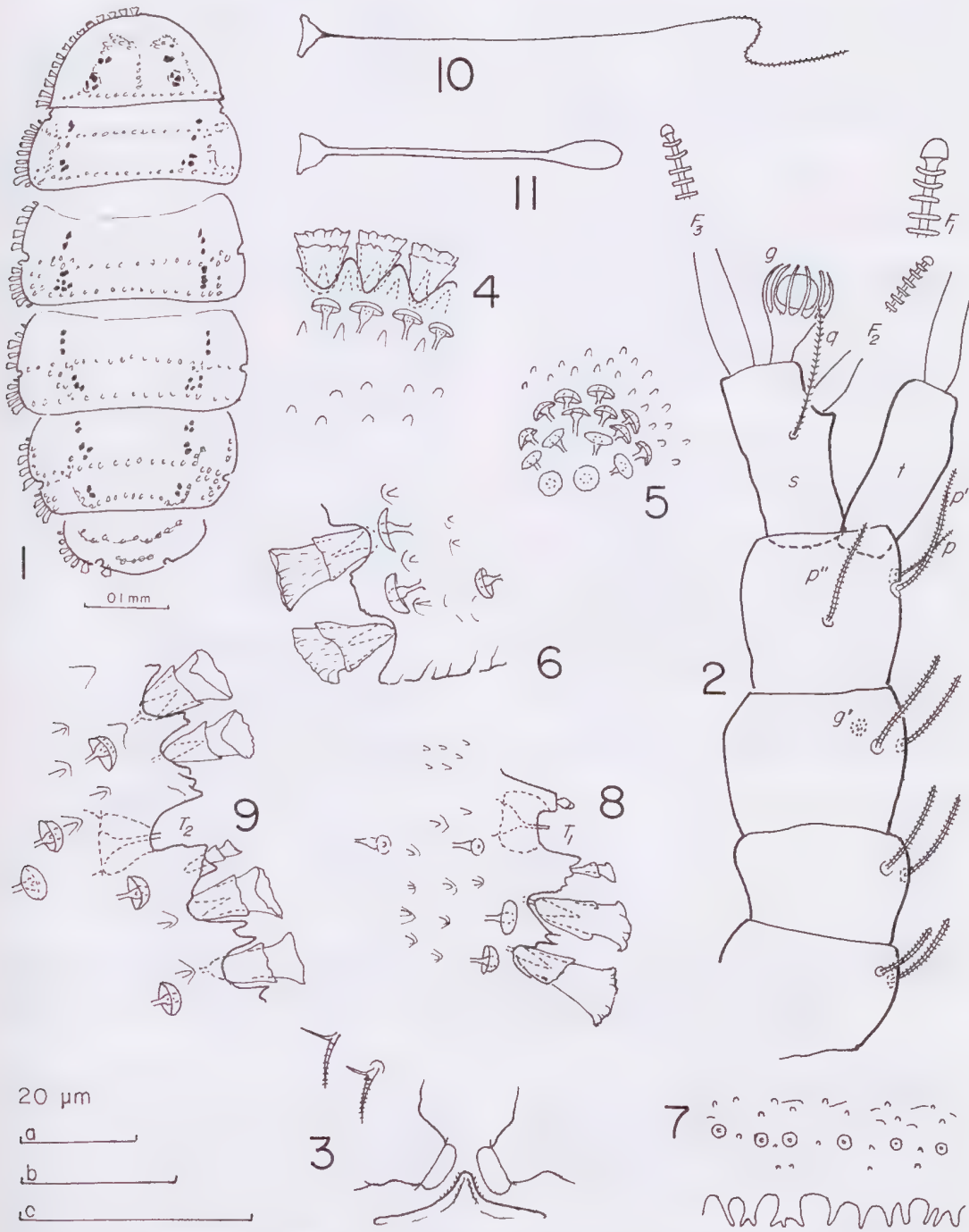
All trichobothria but T_3 with very thin axes, glabrous except for distal half which has erect minute pubescence; distal part curled up (Figure 10); T_3 with thicker axes and distal 1/4 forming clavate swelling (Figure 11). Length of trichobothria: $T_1 = 77$, $T_2 = 80$, $T_3 = 42$, $T_4 \approx 60$, $T_5 = 55 \mu\text{m}$. Ratio $T_3/T_2 = 0.5$.

Legs. Setae on coxa (Figure 17) and trochanter of leg 9 similar, furcate, branches thin, tapering, pointed, pubescent-striate; secondary branch only very little shorter than primary branch. More anteriorly the secondary branch is very short and glabrous.

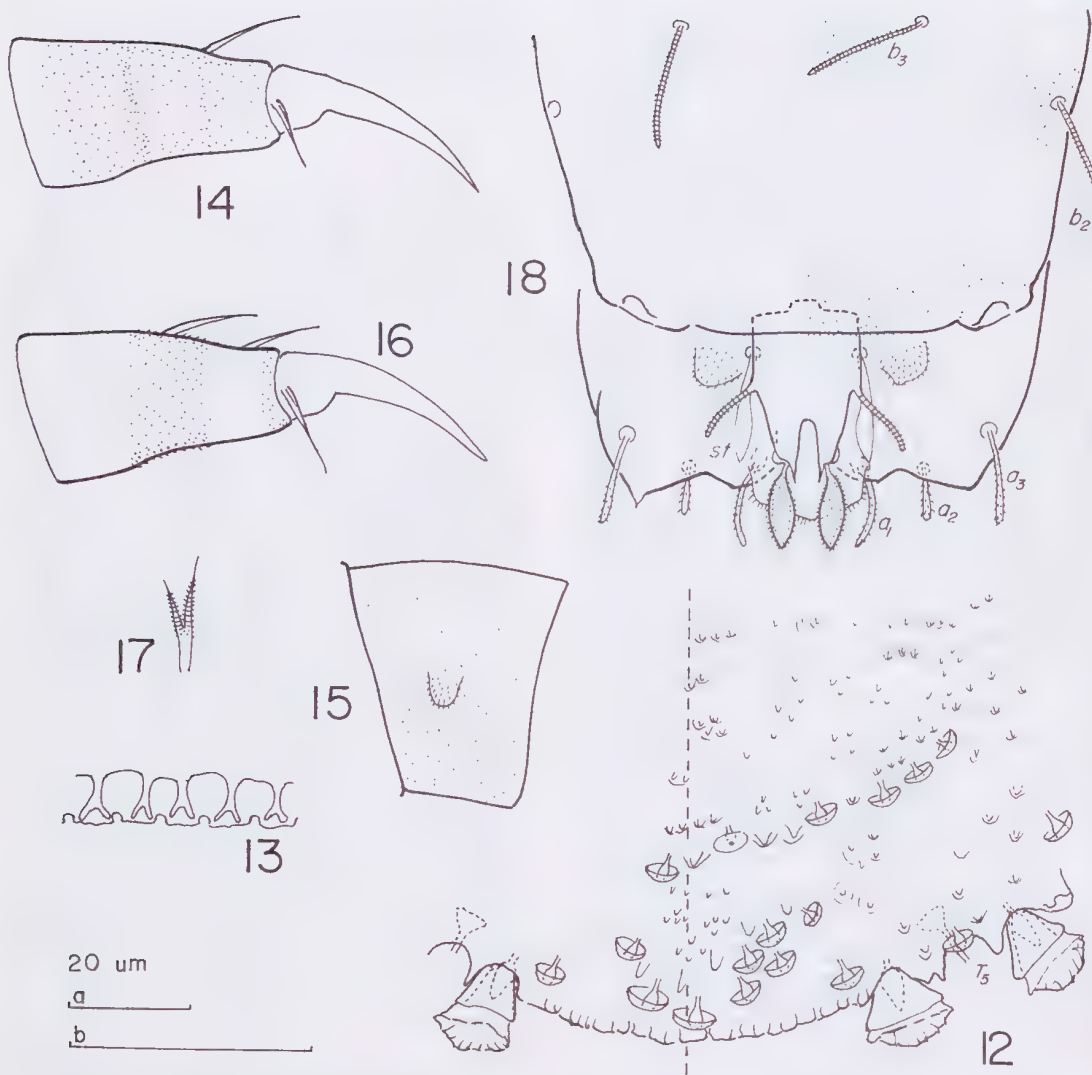
Tarsi tapering, those of leg 9 (Figure 16) 1.5 times as long as greatest diameter; two subsimilar tergal setae, both pointed, glabrous; length of proximal one = 8, distal one = 7 μm ; proximal one 0.6 of the length of tarsus and 1.1 times as long as distal one.

Length of main claw in leg 1 = 20 μm , about as long as tarsus (Figure 14), secondary claw = 6 μm . One seta only on tarsi of leg 1. On anterior side of femur of leg 1 a small linguiform plate (Figure 15), length almost 0.2 of the length of femur; plate with dense short oblique pubescence. Cuticle of anterior legs minutely granular, that of the posterior legs shortly pubescent.

Pygidium (Figure 18). *Tergum.* On its sternal side between st a linguiform plate which protrudes backwards, its posterior triangular part extends as far as the posterolateral corners of the tergum; posterior margin with deep triangular depressions outside the linguiform plate. Setae a_1 cylindrical, curved inwards, with short pubescence; a_2 straight,



Figures 1–11 *Samarangopus papuensis* sp. nov., holotype, adult ♀: 1, Body with tergites I–VI, marginal protuberances drawn on left side only, black patches – tergite warts. 2, Right antenna, sternal view. 3, Collum segment, median and right part, sternal view. 4–7, Tergite I: 4, anterior margin with 3 large marginal protuberances; 5, anterior part of submedian hump; 6, left posterolateral corner; 7, posterior margin. 8, Tergite II, anterolateral part with insertion pit of T1. 9, Tergite III, lateral part with insertion pit of T2. 10, T1. 11, T3. Scale a: 4,5,6,7,8,9; b: 3,10,11; c: 2.



Figures 12–18 *Samarangopus papuensis* sp. nov., holotype, adult ♀: 12. Tergite VI, right half. 13. Tergite IV, posterior margin. 14. Tarsus of leg 1. 15. Femur of leg 1 with linguiform plate, right side, anterior view. 16. Tarsus of leg 9. 17. Seta on coxa of leg 9. 18. Pygidium, sternal view. (Pubescence only partly drawn in 16 and 18). Scale a: 12,13; b: 14,15,16,17,18.

somewhat clavate, with distinct pubescence; a_3 somewhat diverging, cylindrical, blunt, with oblique pubescence; *st* lanceolate, glabrous. Index of tergal setae: $a_1 = a_3 = 8$, $a_2 = 4.5$, $a_1 - a_1 = 8.5$, $a_2 - a_2 = 19$, $a_3 - a_3 = 30$; $st = 10$, $st - st = 9 \mu\text{m}$; $st - st / a_1 - a_1 = 1.1$, $a_1 / a_1 - a_1 = 0.9$, $a_1 / a_1 - a_2 = 1.6$, $a_1 - a_1 / a_2 - a_3 = 1.4$. Cuticle glabrous.

Sternum. Posterior margin between b_1 almost straight; the b_1 of its posterolateral corners missing; b_2 and b_3 cylindrical, striate, curved somewhat inwards and diverging. Anal plate 1.4 times as long as broad, strongly tapering posteriorly; lateral margins with a pair of thin, diverging, cylindrical,

striate branches which are 0.5 of the length of plate; posterior third divided lengthways by a narrow U-shaped incision into two tapering appendages with straight margins, ends of appendages with thorn-like prolongation of inner margins; posterior appendages with stalked bladders which are pointed distally and covered with a short but dense pubescence; bladders 3 times longer than wide, 0.5 of the length of plate.

Remarks

The genus *Samarangopus* has long been considered to be poor in species but collections in

later years with different types of automatic apparatus have yielded much material which has doubled the number of species from seven to fourteen (Scheller 1993, 1994, 1995). The genus does not seem to occur outside of the tropics where its known range includes Thailand and several islands from Madagascar to New Caledonia.

The new species may be most close to *S. umbonifer* Scheller (1995) from Thailand. These two species are generally alike and have specific characters which do not occur in other species, viz. the occurrence of a collar on at least some of the large protuberances of the tergites and the specific shape of the fungiform protuberances there. Good distinguishing characters are the morphology of the tergites II–V (with low sublateral ridges lengthways in *S. papuensis*, with many distinct depressions on each tergite in *S. umbonifer*, the shape of the large marginal protuberances of the tergites (more or less campanulate with square ends, not leaf-shaped), the shape of the sternal antennal branch *s* (wide and cylindrical, not distinctly narrower in distal part) and the shape of some setae (those on coxa and trochanter of leg 9 pointed, not cylindrical; pygidial *a*₃ cylindrical and blunt, not tapering and pointed).

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Manuscript received 30 November 1995; accepted 12 March 1996.

Australian Aborigines and meteorites

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Abstract – Numerous mythological references to meteoritic events by Aboriginal people in Australia contrast with the scant physical evidence of their interaction with meteoritic materials. Possible reasons for this are the unsuitability of some meteorites for tool making and the apparent inability of early Aborigines to work metallic materials. However, there is a strong possibility that Aborigines witnessed one or more of the several recent (< 5000 yrs BP) meteorite impact events in Australia. Evidence for Aboriginal use of meteorites and the recognition of meteoritic events is critically evaluated.

INTRODUCTION

The ceremonial and practical significance of Australian tektites (australites) in Aboriginal life is extensively documented (Baker 1957 and references therein; Edwards 1966). However, despite abundant evidence throughout the world that many other ancient civilizations recognised, utilized and even revered meteorites (particularly meteoritic iron) (e.g., see Buchwald 1975 and references therein), there is very little physical or documentary evidence of Aboriginal acknowledgement or use of meteoritic materials. In view of the prolonged, skilful and widespread use of a variety of natural materials by Aborigines in antiquity, the apparent absence of the use of meteorites in their culture is enigmatic.

Such scant evidence that exists of possible Aboriginal recognition of meteorites in Australia is circumstantial and indirect. The purpose of this paper is two-fold: firstly, to review, critically, the available evidence of the possible recognition of meteorites by Aborigines; and secondly, to present evidence from Western Australia suggesting that there may have been some use of meteoritic materials, particularly in the Nullarbor Region.

The evidence of possible Aboriginal recognition of meteorites can be grouped into three main categories: Aboriginal description of meteoritic events and sites, transport of meteorites from their sites of fall, and utilization of meteoritic materials. Examples of these three categories are listed under the relevant State and Territory below. Those geographic localities mentioned in the text are shown in Figure 1.

BACKGROUND

Meteorites have been found throughout

Australia, although for climatic and physiographic reasons they are rarely found in tropical Australia. The history of the recovery of meteorites in Australia has been reviewed by Bevan (1992). Within the continent there are two significant areas for the recovery of meteorites: the Nullarbor Region, and the area around the Menindee Lakes of western New South Wales. These accumulations have resulted from prolonged aridity that has allowed the preservation of meteorites for thousands of years after their fall, and the large numbers that have been recovered are a direct result of their ease of recognition in those environments. Most meteorites are dark rocks and in areas like the Nullarbor they stand out as unusual against the pale indigenous limestone. Bevan (1992) has suggested that similarly dense accumulations of meteorites are likely to occur throughout the arid zone of Australia. However, recognition of these objects in most terrains is hampered by local physiography (e.g., sand dunes) and naturally dark, or 'rusty-looking' country rocks.

Three main groups of meteorites are recognised, determined by the relative amounts of metallic nickel-iron and ferro-magnesian silicates they contain. *Irons* are composed almost entirely of metal; *stones* are made predominantly of silicates (olivine, pyroxene and feldspar) similar to those occurring in terrestrial basalts, but may also contain appreciable amounts of metal; and *stony-irons* are mixtures of metal and silicates in roughly equal proportions. Stony meteorites are the most common, accounting for more than 95% of those seen to fall, whereas irons and stony-irons are rare, accounting for around 4% and 1% of meteorites seen to fall, respectively. In terms of collections, however, irons are often over-represented. For



Figure 1 Geographic locations and meteorite sites mentioned in the text.

example, of all the meteorites found in Australia, irons account for approximately 29% of the total. This is the result of human collection bias. The more exotic-looking irons are easily recognised as meteorites and, in modern times, have been preferentially collected.

In the population of meteorites from the Nullarbor Region of Australia, however, only four iron meteorites and one stony-iron meteorite are recorded. While these account for more than 90% of the mass of all meteorites recovered from the region, Bevan (1992) noted that taken by type, and as a percentage of the total population of meteorites so far recorded, the irons and stony-irons were under represented in the Nullarbor by about a factor of two compared with the modern flux of meteorites.

The low percentage of metallic meteorites in the Nullarbor population is difficult to explain. In the Nullarbor in modern times, many meteorites have been found by inexperienced personnel and it

would be expected that any bias would be towards more, rather than less, iron meteorites. A complicating factor is that the Nullarbor has been periodically populated by Aboriginal people over at least the last 20,000 years (e.g., see White and O'Connell 1982), and by itinerant prospectors and rabbiters within the last 100 years. Human interference (possibly Aboriginal) with the population of meteorites from the Nullarbor, by the selective collection of irons, cannot be ruled out.

ABORIGINAL DESCRIPTION OF METEORITIC EVENTS AND SITES

Northern Territory

Henbury Craters

The best example in Australia of possible Aboriginal recognition of a meteoritic event is the

group of Henbury craters (24°35'S, 133°10'E) and associated meteorites situated near the Finke River in the Northern Territory. The craters, formed by the impact of an iron meteorite, were recognised as meteoritic by Europeans in 1931 (Alderman 1932a,b). Buchwald (1975) estimates that more than 1,200 kg of iron meteorites have been recovered from the craters and surroundings, the bulk being collected before 1933 (Graham *et al.* 1985).

Measurement of the activities of the radioisotopes Cl^{36} and C^{14} in the Henbury meteorite by Goel and Kohman (1963) and Kohman and Goel (1963), respectively, show that the impact event occurred less than 5,000 yrs BP. It is significant that this age is well within the currently proposed time (50,000 yrs BP) of Aboriginal occupation of Australia (Roberts *et al.* 1990).

Alderman (1932a) noted that inquiries from Aborigines in the district revealed that none had any ideas as to the origin of the craters. However, in an addendum to Alderman's 1932 (a) paper, L.J. Spencer communicated a report from Mr R. Bedford of the Kyancutta Museum that a local prospector (J.M. Mitchell of Oodnadatta) asserted that local Aboriginal people described the locality as "*Chindu chinna waru chingi yabu*" which translates as "*Sun walk fire devil rock*". This description suggests that it is quite possible that the ancestors of the people with whom Mitchell spoke witnessed the fall and impact of the Henbury meteorite. However, in contradiction to this view, Mountford (1976) recounts the southern Aranda myth of the lizard-woman, *Mulumura*, in relation to the Henbury meteorite craters. According to the myth, the largest of the Henbury craters was the camping place of a menstruating *Mulumura* lizard-woman. When the sand on which *Mulumura* was resting became saturated with blood, she picked it up and threw it away; the crater was thus created and the piles of meteoritic iron surrounding the crater represented the blood-stained earth. Mountford (1976) suggests that the myth shows that the Aborigines have no memory of the impact event that created the large crater, though qualifies his conclusion by noting that he did not obtain any myths accounting for the other craters, and that there was little doubt that other myths existed.

Magellanic Clouds

Mountford (1976) describes a myth of the Ngalia people of the Northern Territory concerning the Magellanic Clouds. The myth deals with two men, the *Walanari*, who ate the *kurunba* (spirit) of a dead man during the time of creation. Afterwards, the *Walanari* rose into the sky and made their camps in the Magellanic Clouds, from where they act as both helpers of the law-abiding, and punishers of evil-doers. The Ngalia believed that meteors were glowing stones thrown to Earth by the *Walanari*.

New South Wales

The Paakantji (Bakendji) people of western New South Wales record an ancient event that is reported to have occurred at a place along the Darling River between Wilcannia and Mount Murchison (Jones 1989). A bend in the river is called "*purli ngaangkalitji*", meaning "*the fallen star*". According to the legend, a group of people were camped at the location when "*they heard this rumbling noise from the sky, like thunder... and as it [the falling star] came down there was red streaks, and a great big ball of fire coming down... and there was smoke....*" (Jones 1989). The Paakantji account continues thus, "*and where it fell, some of them died there and some of them got burnt.... there was fire in it. The ones that weren't too badly burnt, they got away. The others died there....*"

This description of the event suggests that ancestors of the Paakantji people witnessed the fall of a large meteorite, and the account of the impact indicates a crater-forming or Tunguska-type, event. According to the legend the event was followed by a deluge. However, no evidence of an impact crater or meteoritic material occurs at the site indicated in the legend (Steel and Snow 1991: 5). It is quite possible that the site on the Darling River is where the legend was recounted, but that it was not the actual site of the recorded event.

South Australia

In reference to the description of the passage of a large meteor across the sky, Tindale (1974) notes that the Ramindjeri people of Encounter Bay (35°35'S, 138°45'E) visualised the event as the flight of an evil being named "*Mulda*", who was a harbinger of sickness and blindness.

Western Australia

Wolfe Creek Crater

The Wolfe Creek meteorite crater in the Kimberley of Western Australia has been dated at 300,000 yrs BP (Shoemaker *et al.* 1990). Therefore, the formation of the crater pre-dates the known human occupation of Australia and is unlikely to have been witnessed. Wolfe Creek Crater is an example where no recognition is afforded by Aboriginal tradition of the meteoritic origin of the site. The local Djaru people call the locality "*Kandimalal*". Their mythology speaks of two rainbow snakes, whose sinuous paths across the desert formed the nearby Sturt Creek and Wolfe Creek (Bevan and McNamara 1993). The crater represents the place where one of the snakes emerged from the ground. No mention is made in the Djaru account of the association of meteorites that occurs at the crater, and it is interesting to note that their mythology attributes the origin of the crater to events within the Earth rather than from above it.

Locality unknown

Artists from the Wirrimanu (Balgo) community of Western Australia have a tradition depicted in painting representing the fall of a 'star'. Brief accounts of the event are recorded and sold with the painting. The story recalls a 'star' that fell out of the sky into Lake Mackay. The story continues that 'the Rainbow snake came to this place and ate up a lot of people'. No large meteorite fall is known in the area of Lake Mackay. However, it is interesting to note that a line from Balgo projected through Lake Mackay passes close to the McDonnell Ranges and the site of the Henbury craters.

Another Kimberley people, the Wolmeri, have a myth that Venus 'the star' came to Earth and left a stone in one of the horde countries (Kaberry 1939: 12).

In the myths of the Wheelman Tribe of the south-west of Western Australia, Hassle (1934) notes that they believed that in the Milky Way "one cluster of stars visited another and occasionally stars got lost and fell down to earth as we see them do even now".

RECOGNITION OF METEORITES, AND TRANSPORT FROM THEIR SITES OF FALL

Well-documented examples of the recognition of meteorites by Aborigines are listed below. In addition, there are numerous possible examples documented of transport of meteorites in Australia by human agency (e.g., see Buchwald 1975; Graham *et al.* 1985). Many of these are fragments of the Henbury meteorite that were found considerable distances from the site of the craters, and the occurrences of which cannot be accounted for by the processes of nature. To date, no conclusive proof exists that any of these meteorites was transported by Aborigines. However, that the meteorites have been transported by human agency subsequent to their fall is not doubted. Other examples are less convincing, although circumstantial evidence suggests possible Aboriginal recognition of, and interaction with meteoritic materials.

Northern Territory

Henbury meteorite (fragments found at Basedow Range, Nutwood Downs and Gallipoli Station)

One of the earliest recognised examples of human transport of a meteorite in Australia was a mass of iron meteorite weighing a few kilograms found 6.5 km from Willbia Wells along the south side of the Basedow Range in the Northern Territory. The locality lies about 85 km southwest of the Henbury craters, and the meteorite was considered by Hodge-Smith to be one of the Henbury masses that had been transported by

human agency, most likely Aboriginal (letter in the Smithsonian Institution, Washington, of 1 April 1958 from R. O. Chalmers, Australian Museum, Sydney). Additional fragments of iron meteorites reportedly found at Nutwood Downs (ca. 15°49'S, 134°09'E) and Gallipoli Station (ca. 19°08'S, 137°53'E) have also been suspected to be fragments of Henbury (Buchwald 1975). Subsequent chemical analysis by Scott *et al.* (1973) and detailed metallographic examination by Buchwald (1975) has shown, beyond reasonable doubt, that the meteorites found at Basedow Range, Nutwood Downs and Gallipoli Station are all fragments of the disrupted Henbury projectile. When these were transported from the site of the craters is unknown.

Several other genuine fragments of the Henbury meteorite have recently been reported from localities as far afield as Arnhem Land in the Northern Territory, and inter-state in Queensland (Bevan *in prep.*). It has also been suggested by Buchwald (1975) that the Nuleri meteorite found in Western Australia (27°50'S, 123°52'E) may be a transported fragment of Henbury, although this has yet to be proved. Other examples of transported fragments of Henbury are held in the collections of the Northern Territory Museum in Darwin (D. Megirian *pers. comm.*).

Huckitta meteorite (Alice Springs fragment)

In 1924, a 1084 g fragment of a rare stony-iron meteorite type (pallasite) was found by H. Basedow on the Burt Plains (23°33'S, 133°52'E) near Alice Springs. The so-called *Alice Springs* meteorite was described by Spencer (1932a). However, in July 1937, the main mass of 1411.5 kg, of which the *Alice Springs* meteorite is evidently a transported fragment, was located at Huckitta (22°22'S, 135°46'E) surrounded by a large quantity of iron-shale representing the weathering products from the mass. (Madigan 1937, 1939; Megirian *et al.* 1987). The *Alice Springs* fragment of the Huckitta meteorite was clearly transported by human agency prior to 1924.

Evidence that transportation of the Alice Springs fragment by Aborigines may have occurred is circumstantial. Megirian *et al.* (1987) estimate a terrestrial age for the Huckitta meteorite of >18,000 yrs and the deeply weathered nature of the mass on its discovery is consistent with prolonged exposure to weathering (Madigan 1939). Madigan's (1939) account of the discovery of the meteorite by Europeans suggests that local Aborigines were previously well aware of the existence of the mass. Madigan (1939) had recognised the meteorite from a fragment that had been removed from the mass by Mick Laughton, a part-Aborigine employed on Huckitta Station. Whereas the Europeans on the Station were ignorant of the meteoritic nature of the unusual rock, the local Aborigines held the

meteorite in awe, possibly as a sacred and, therefore, fearful thing (Madigan 1939).

Boxhole (Hart Range fragment)

In 1944 a fragment of iron meteorite weighing 608 g was presented by Mr J.S. Foxhall to the Geological Survey of Western Australia. The meteorite was evidently discovered at a locality in the Harts Range some 60 km south of the Boxhole meteorite impact crater (22°37'S, 135°12'E). A detailed study of the *Hart Range* meteorite by De Laeter (1973) has shown that it is a fragment of the Boxhole meteorite. De Laeter (1973) concluded that it was probable that the meteorite had been transported from the crater by human agency. The age of the Boxhole crater (c. 5400 yrs) as determined by Kohman and Goel (1963) is similar to that of the Henbury craters although Wasson (1967) has shown that differences in the chemistry and metallurgy of the impacting meteorites prove that they are two distinct events. Nevertheless, like Henbury, the age of formation of the Boxhole crater is well within the time of Aboriginal occupation of Australia and the event may have been witnessed.

New South Wales

Yandama and Cartoonkana meteorites

A mass of stony meteorite weighing 5.8 kg was acquired by the South Australian Museum in 1914 from Mr T.F. Gill. The exact date of find is unknown. In his description, Alderman (1936) notes that the meteorite named Yandama was found at "Blacks' Camp, Big Plain, Yandama Station, NSW" (29°45'S, 141°02'E). Alderman (1936) also noted that the meteorite has a fractured surface that "*indicates the possibility of the stone, as found, having one time formed part of a considerably larger mass*".

An additional stone weighing 290 g was also found before 1914 in the same general area as the Yandama meteorite and was named Cartoonkana (Alderman 1936). It has since been suggested by Mason (1974) on the basis of classification that the Yandama and Cartoonkana meteorites could be fragments of the same meteorite. Interestingly, the localities of both the Yandama and Cartoonkana finds lie close to an old Aboriginal camp. However, the possibility that the meteorites may have been broken from the same mass by Aborigines and then distributed cannot be substantiated.

Western Australia

Mt Dooling (Gosnells fragment)

Three masses of an unusual iron meteorite (Mount Dooling) found in Western Australia between 1909 and 1979 have been shown to belong

to the same fall (De Laeter *et al.* 1972; De Laeter 1980). Two large masses weighing 31.5 kg (found 1909) and 701 kg (found 1979), respectively, were found just to the east of the Mount Manning Range (30°00'S, 119°40'E) approximately 430 km north east of Perth, whilst a third mass, weighing 1.5 kg, was found in 1960 near the Perth suburb of Gosnells on the edge of the Darling escarpment (32°05'S, 116°01'E) some 19 km south east of the city centre. De Laeter *et al.* (1972) demonstrated convincingly that the *Gosnells* meteorite was a fragment broken from the 31.5 kg mass of the Mount Dooling meteorite prior to its discovery (1909) and transported by human agency, although they concluded that it was not known when, or by whom.

The *Gosnells* meteorite fragment was found in bushland. McCall (1972) and De Laeter and Bevan (1992) suggest that transport of the *Gosnells* mass from the Mount Manning area to Perth by Aborigines is one possible explanation as to how the fragments became so widely displaced.

Dalgaranga (Murchison Downs fragment)

Recently, Bevan and Griffin (1994) have shown that a small metallic slug, weighing 33.5 g, found near Murchison Downs Station (26°40'S, 119°00'E) in 1925 is a transported fragment of the stony-iron meteorite that formed the Dalgaranga meteorite impact crater. The distance between the reported find-site of the Murchison Downs meteorite and the Dalgaranga crater is *ca.* 200 km. Bevan and Griffin (1994) suggest that the *Murchison Downs* fragment has been transported by human agency, and may have been transported by Aborigines.

The age of formation of the Dalgaranga crater is variably reported to be between 3000–27000 yrs BP (Shoemaker and Shoemaker 1988; Grieve 1991). Like the Henbury craters, these ages lie well within the known Aboriginal occupation of Australia and the formation of the Dalgaranga crater may have been witnessed by Aborigines. However, we have been unable to discover any references to this occurrence in Aboriginal myths.

Mundrabilla (Tookana Rockhole fragments)

The Mundrabilla meteorite shower, including the largest meteorite (11.5 tonnes) recovered from Australia, occurs over a large strewnfield more than 50 km long in the central Western Australian Nullarbor Plain (De Laeter 1972; De Laeter and Cleverly 1983; Bevan and Binns 1989). Some twelve large masses totalling more than 22 tonnes of this shower are in collections around the world (Graham *et al.* 1985; Bevan and Binns 1989). Additionally, thousands of smaller fragments of the same meteorite shower are known which have characteristic rounded, "knuckle-bone" shapes. On the basis of Al²⁶ and Be¹⁰ activity, the age of the fall

of the Mundrabilla meteorite shower is estimated by Aylmer *et al.* (1988) to be >1 Myr BP.

Most fragments of the Mundrabilla iron are found within an area straddling the Trans-Australian Railway between the townships of Forrest and Loongana. However, De Laeter and Cleverly (1983) reported the discovery in 1978, by the late Mr A.J. Carlisle, of about 100 small fragments of the Mundrabilla meteorite near *Tookana Rock Hole* (31°41'S, 128°21'E) situated 47 km NNW from Eucla on the Eyre Highway. The *Tookana Rock Hole* locality lies approximately 135 km to the SE of the main strewnfield of the Mundrabilla meteorite. De Laeter and Bevan (1992) suggest that the *Tookana Rock Hole* material had been transported from the Mundrabilla area by human agency, almost certainly Aborigines.

The heaviest specimen found at *Tookana Rock Hole* weighed 0.44 kg and the total mass of the recovered material was 3.97 kg. When the fragments were discovered, the finder reported that they were scattered over an area about 10 m in diameter. De Laeter and Cleverly (1983) concluded that the material represents the disintegration, by weathering, of a mass of around 5 kg. Moreover, De Laeter and Cleverly (1983) discount the possibility of human transport on the grounds that the state of weathering (apparently *in situ*) of the material suggests that transport must have occurred long before Europeans reached the area, and that Aborigines were not known to have used meteorites. While the observations of De Laeter and Cleverly (1983) appear to rule out transport of the meteorite by Europeans, they do not exclude the possibility of transport of the material by Aborigines in antiquity.

Queensland

Thunda meteorite

A mass of iron weighing 62 kg was known before 1881 at Thunda (25°42'S, 143°3'E) near Windorah in the Diamantina district of Queensland. The mass, originally buried in the ground had been known to Aborigines for some time and covered by them with stones before its recognition by Europeans (Liversidge 1886; Spencer 1937). According to Spencer (1937), two masses of iron, the "Old Man" and the "Old Woman" were known to Aborigines on Githa Creek. In 1881, the "Old Woman" mass was taken to the Thunda Homestead about 25 km to the north of the site of discovery. The whereabouts of the "Old Man" mass are unknown. Half of the 62 kg "Old Woman" (Thunda) mass is deposited in the Natural History Museum in London.

Victoria

Cranbourne meteorite

Among the earliest well-documented recoveries

of meteorites in Australia were two large masses of iron weighing 3.5 and 1.5 tons found in 1854 near Cranbourne in Victoria (Walcott 1915). During the period 1854–1928, eight additional masses of the same meteorite shower were recovered from an area between Beaconsfield and Langwarrin bringing the total weight recovered to more than 10 tons. Walcott (1915) noted from reports of people who had visited the site that the largest meteorite was originally buried in the ground with a small portion protruding above it. Old colonists are reported to have recounted a time when Aborigines used to dance around the meteorite, "*beating their stone tomahawks against it, and apparently much pleased with the metallic sounds thus produced*" (Walcott 1915).

Locality unknown

Barker (1964) refers to the recognition of a meteoritic mass by Aborigines at an unknown locality. In his words;

"The blacks knew of a meteorite out in the desert, knew exactly what it was, how it fell and, in spite of their scientific ignorance, could describe it correctly, leaving no shadow of doubt that it was really there. But it was serving too useful a purpose where it was, a source for myths and superstitions that could be used to the benefit of the old people. So they would not reveal its whereabouts to any whites, though they were always willing to talk about it"

UTILIZATION OF METEORITIC MATERIALS BY ABORIGINES

While there are numerous, well documented examples of the discovery of meteorites in modern times by Aboriginal people (e.g., see Hodge-Smith 1939; McCall and De Laeter 1965), currently, there are no known examples of the use of meteoritic materials by Aboriginal people in antiquity. Some problems arise from the confusion that exists in the non-meteoritical or non-geological literature in distinguishing genuine meteorites from tektites. For example, 'tektites' are commonly referred to by modern Aboriginal people as 'meteorites'. An example of this confusion, which is not confined to Aborigines, is well illustrated by Barker (1964);

"In the desert country in the west of South Australia were hundreds of little round meteorites [sic], about the size of a pigeon's egg. Again the blacks knew what they were and stuck rigidly to their theory but white people were inclined to disbelieve. Now scientists are satisfied that the blacks were right, and these tiny black and shiny meteorites [sic] called australites or, more correctly, tektites can be seen in most museums"

DISCUSSION

In areas such as the Nullarbor Region, the available country rock is limestone. Field evidence from this region indicates that the majority of the discarded implements to be found there were brought into the region from outside. However, the Nullarbor contains one of the world's richest accumulations of meteorites, which are easily recognised in that terrain (Bevan 1992). Irrespective of whether the indigenous Aborigines of the Nullarbor (the Mirning people) understood the extra-terrestrial nature of meteorites or attached any other significance to them, it seems inconceivable that they could have ignored this resource without investigating the potential of meteorites for practical purposes.

In terms of their practical value, although meteoritic materials are unusually dense, many meteoritic stones are weak, friable materials and are not as resilient as many terrestrial igneous and sedimentary rocks such as granites, basalts, gabbros and quartzites. For this reason, aside from their rarity, meteoritic stones would have been generally of less practical use to Aborigines in antiquity than the more abundantly available terrestrial rocks. Nevertheless, some highly crystalline stony meteorites are equally suitable as some terrestrial igneous rocks for the manufacture of implements.

Large iron meteorites cannot be moved easily, and Aborigines lacked the technology to remove small samples from compact iron meteorites that did not have natural cracks or fissures. Small iron meteorites could not be worked easily, although some, such as the abundantly available Mundrabilla irons, could have been used as throwing-stones. Because of their nickel contents (generally 5–25 wt % Ni) meteoritic iron is reasonably malleable and can be hot and cold worked. A number of examples of working of material in antiquity in other parts of the world, notably the Inuits of Greenland and the Hopewell Indians of America, are documented in the literature (see Buchwald 1975).

However, Australian Aboriginal 'use' of objects extends beyond simple mechanical useage. Odd stones, such as tektites, were often collected and used as sacred objects, charms and healing stones (Baker 1957). A similar use of meteorites is suggested by the Huckitta, Thunda and Cranbourne meteorite examples, and by the unlocated example documented by Barker (1964).

SUMMARY AND CONCLUSIONS

Where clear recognition of meteoritic events and sites is afforded by Aboriginal legend, descriptions consistently convey a theme of awe and fear. Meteoritic masses or their impact sites, real or

perceived, were to be avoided. Strehlow (D. Hugo, *pers. comm.*) notes that the Aranda of central Australia saw meteorites (meteors) as large venomous snakes called *kulaia*, with big fiery eyes. These fly through the air and fall into deep waterholes, for which reason the latter were to be avoided. However, it is interesting to note that rather than having heavenly origins, most celestial phenomena were believed by people such as the Aranda and Ngalia of central Australia, originally to have ascended into the skies from an earth-born existence (D. Hugo, *pers. comm.*). Nevertheless, the *Walanari* myth suggests that the Ngalia did indeed have knowledge of meteors and meteorites, and perhaps other astronomical objects.

It is not known whether Aborigines witnessed the actual impact of the crater-forming meteorite at the site now known as Henbury. From evidence provided by Mitchell in Alderman (1932a) that is descriptive of the kinds of phenomena expected with such a devastating event, it is possible that they did witness the impact. However, some of the mythical and legendary associations of meteorite impact structures such as Henbury are remote from descriptions of a cataclysmic event, but equate with a far milder set of occurrences (Mountford 1976). This suggests that in some cases there was no direct connection made by Aborigines between what must have been a spectacular and noisy atmospheric and terrestrial event, and the geological evidence for that event.

In relation to the Henbury craters three questions arise; did Aborigines see the impact as such a terrifying event that they decided to ignore it; were their interpretations subsequently modified by intercourse with Europeans; or did they not see it at all? In the last case it would not be surprising that they failed to attribute the craters to an extra-terrestrial origin, given that these are not common occurrences. Moreover, if Aborigines witnessed the event from a distance, which is likely considering the sparse nature of their population, then they may not have related the atmospheric and terrestrial events.

The discrepancy between Mitchell's account, reported in Alderman (1932a), of Aboriginal understanding of the Henbury craters, Alderman's (1932a) own account and the more traditional myth of the Aranda people documented by Mountford (1976) suggests that European influence may have introduced a meteoritic explanation of the event to the Aborigines that they subsequently adopted. However, a proper understanding of the mechanics of impact cratering was not generally available to meteoriticists until around 1932 (e.g., see Spencer 1932b) and was not popularly published until much later.

The Paakantji example of New South Wales (Jones 1989) seems less equivocal. The description

of the phenomena is entirely consistent with that to be expected to accompany a crater-forming impact. Moreover, the legend is reportedly an ancient one handed down through many generations (Jones 1989). The location of the event remains a mystery, and the possibility that the Paakantji are describing the Henbury occurrence cannot be discounted.

In modern times, when Aborigines were introduced to metal in functional shapes like barrel hoops, or discarded horse shoes and the like, they were quick to adapt this new material to their needs (Akerman and Bindon 1984). Traditionally shaped spearheads, axes and other tools once made in stone were made from pieces of metal obtained from Europeans. Fragments of meteoritic iron, although recognisable as metal, are not generally evocative of tool shapes. Moreover traditional Aboriginal methods of working stone by flaking and grinding, are not applicable to chunks of iron. Although there is some evidence for Aboriginal selection of meteoritic iron objects as things being out of the ordinary, and that they may have been transported from their original place of fall to other locations, no substantial evidence exists of experimental working of iron meteorites by Aborigines during prehistory.

In the Nullarbor where meteorites are easily found (notably the Mundrabilla iron meteorite), grinding was the method used by Aborigines to process grass seeds into a gruel or damper. Although some edge-ground axes do occur here, most of the country rock is sedimentary or is buried at such depth beneath sand that it is generally unavailable to Aborigines. Many of the larger (1cm +) artefacts to be found in the Nullarbor are made from igneous rocks transported from other areas, notably the Giles Complex to the north, or tektites. Consequently, there was no great tradition of edge-grinding in the region. Apart from the amount of work likely to be involved with grinding or beating a chunk of meteoritic iron to the shape of an axe, there is little evidence of a tradition that would lead to this kind of labour intensive modification of a resource. However, the deficit in the number of different iron meteorites recovered from the Nullarbor may be due to human activity.

Notwithstanding, we urge archaeologists and anthropologists throughout Australia to re-examine the extensive collections of Aboriginal artefacts that exist for the possibility that they may contain rare implements and other objects made from stony meteorites.

ACKNOWLEDGEMENTS

We are indebted to David Hugo of the Strehlow Research Centre in Alice Springs for providing information on the unpublished English translation

of Strehlow's work, "Die Aranda – und Loritja-Stämme, Zentral Australien", and to Pat Vinnicombe for providing some material. Thanks are also due to Mance Lofgren and Vagn Buchwald for their helpful reviews and to Danielle Hendricks for drafting the figure.

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Caridina spelunca, a new species of freshwater shrimp (Crustacea: Decapoda: Atyidae) from a Western Australian cave

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Abstract – A new species of freshwater atyid shrimp, *Caridina spelunca* sp. nov., collected from a series of tufa dams within the outflow tunnel of Old Napier Downs Cave in the northern Napier Range, Western Australia, is described and illustrated. It is the first species of *Caridina* to be reported from Western Australia. *Caridina spelunca* sp. nov. can be distinguished from other species of *Caridina* by a combination of the following diagnostic characters: deep cephalothorax (depth about 0.8 times length), relatively small but normal eyes, presence of epipods on the first four pairs of pereopods, lack of a median spine on the posterior telsonic margin and the absence of an appendix interna on the endopod of the first male pleopod.

INTRODUCTION

Although at least seventeen species of atyid shrimps are presently known from Australia (Choy and Horwitz 1995), only three species (*Stygiocaris lancifera* Holthuis, 1960, *S. stylifera* Holthuis, 1960 and *Pycneus morsitans* Holthuis, 1986) have been reported from Western Australia (Holthuis 1960, 1986). All three species are obligate troglobites, with short-stalked, pyriform eyes which are devoid of retinal pigmentation. Most species of the genus *Caridina* are epigean and, although several species have been collected from troglons (subterranean water bodies), only a few of these exhibit troglomorphic characters (Guo *et al.*, 1996). One Australian species, *Caridina thermophila* Riek, 1953 was collected in water from an artesian bore but neither this nor any of the other seven described Australian species of this genus exhibit troglomorphic characters. This paper describes a new species of *Caridina* from Old Napier Downs Cave in the northern Napier Range in the Kimberley, Western Australia. Specimens were collected from a series of freshwater tufa dams within the outflow tunnel of the cave in the twilight zone (Humphreys 1995). These dams are well above the level of the plain and no water was flowing out of the out of the cave when the samples were collected. The lack of troglomorphic characters suggests that this species may be a facultative troglobite.

MATERIALS AND METHODS

The material studied was obtained from the Western Australian Museum, Perth (WAM) and

the Australian Museum, Sydney (AM). The format of the description and morphological terms follow Choy (1991). Cuticle spination and setation terminology follows (Felgenhauer 1992).

Abbreviations used in the text: CL, post-orbital carapace length measured from dorso-lateral invagination of the posterior margin to orbital margin of carapace; RL, pre-orbital rostral length measured from orbital margin of carapace to tip of rostrum; SL, body length from tip of telson to orbital margin of carapace; \bar{x} , mean value; s.e., standard error.

SYSTEMATICS

Family ATYIDAE De Haan, 1849

Caridina H. Milne Edwards, 1837

Caridina spelunca sp. nov.

Figure 1

Caridina sp. nov.: Humphreys, 1995: 57.

Material Examined

Holotype

Adult ♂, Karst KN-1, Old Napier Downs Cave, Western Australia, Australia, 17°14'S 124°39'E, 12 July 1994, W.F. Humphreys (WAM 422–95), 13.2 mm SL, 3.48 mm CL, 1.72 mm RL.

Allotype

Adult ♀ Karst KN-1, Old Napier Downs Cave, Western Australia, Australia, 11 July 1994, B. Vine (WAM 423–95) 15.8 mm SL, 3.64 mm CL, 1.69 mm RL.

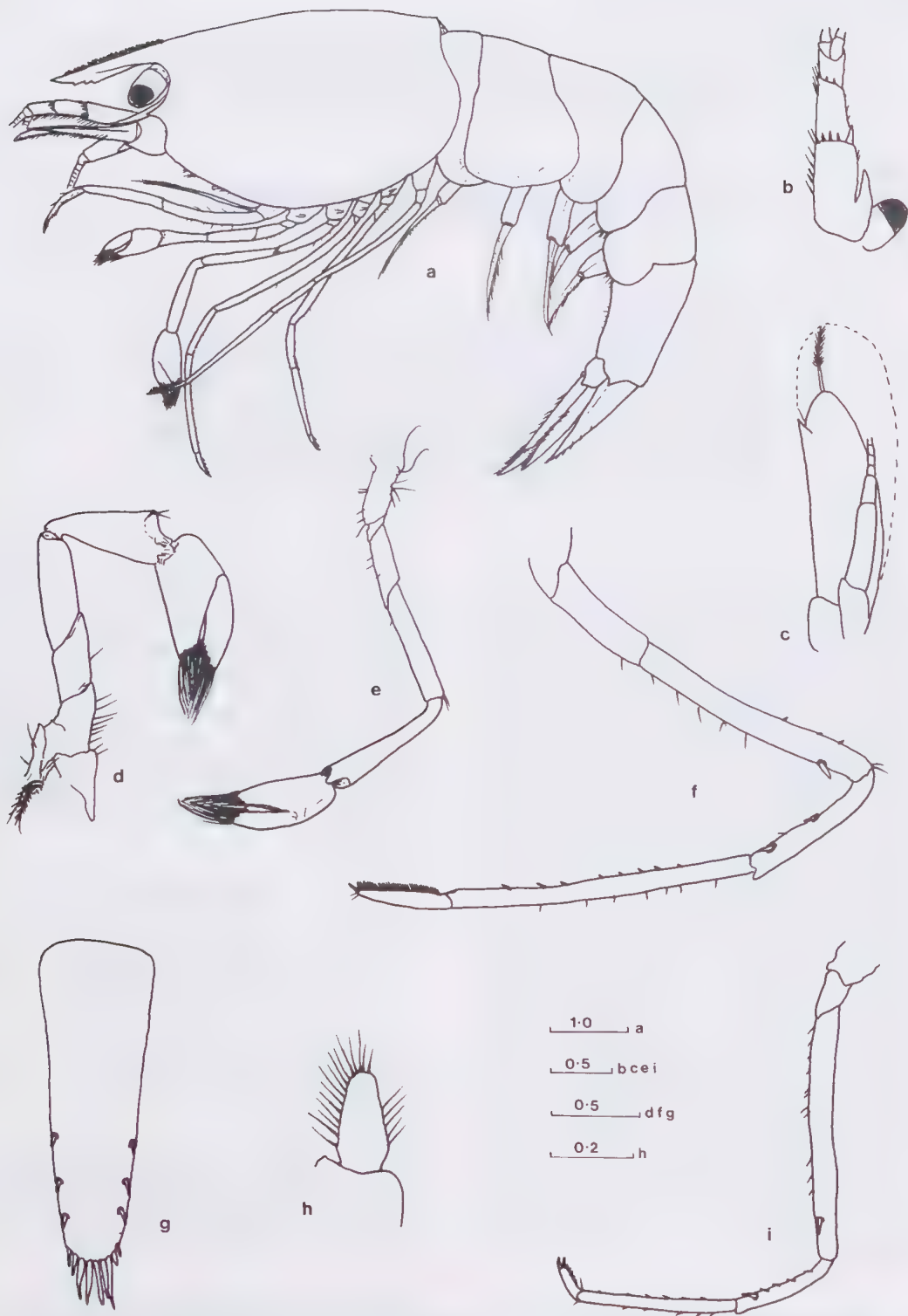


Figure 1 *Caridina spelunca* sp. nov.: a, body, lateral aspect; b, antennule and eye; c, antenna; d, first pereiopod; e, second pereiopod; f, fifth pereiopod; g, telson; h, endopod of first male pleopod; i, third pereiopod. Scale in mm.

Paratypes

Australia: Western Australia: 1 juvenile ♀, Karst KN-1, Old Napier Downs Cave, 9 June 1966, A. Douglas and G. Kendrick (WAM 424-95), 1.79 mm CL; 2 ♂, 1 ♀ same collection data as holotype (WAM 425-95), 3.00-3.60 mm CL; 1 ♀ same locality as allotype (WAM 426-95), 3.38 mm; 8 poorly preserved specimens, str. K10, outer pool, Old Napier Cave, 17°14'S 124°41'E, water depth ca. 1 m, water clear, pH 7.66, substrate mainly limestone rock with some loose rocks, gravel and sand, outermost pool also with tree roots, water temperature 20°C in outermost pool and 28°C in innermost pool that could be easily reached, outermost and adjacent pools contained shrimps, 3 July 1988, W.F. Ponder (AM P.38512); 1 ♀, same data (AM P.40859), 2.9 mm CL; 1 ♂, same data (AM P.40856, ex P.38512), 1.9 mm CL.

Diagnosis

Small atyid shrimp with deep cephalothorax and small but well developed eyes; rostrum laterally compressed, dorsally and ventrally toothed, lateral carina ending before apex; epipods on first four pairs of pereopods; telsonic margin without median spine; endopod of first male pleopod without appendix interna.

Description

Body (Figure 1a) small, subcylindrical; males in collection up to 13.2 mm SL, females up to 15.8 mm SL.

Carapace (Figure 1a) glabrous, depth 0.68-0.9 CL; rostrum short, 0.37-0.49 CL, length 6.1-6.5 X height, curving downward, reaching tip of second antennular segment, 11-24 dorsal rostral teeth (\bar{x} = 18, s.e. = 1.33), 0-4 (\bar{x} = 2.6, s.e. = 0.4) situated behind posterior orbital margin, setose, 0-4 (\bar{x} = 2.7, s.e. = 0.4) ventral rostral teeth; lateral carina dividing rostrum into two unequal parts, continuing anteriorly from orbital margin to about 0.7 of rostrum; antennal spine short, strong, placed on lower orbital angle; pterygostomial angle obtuse, pterygostomial spine absent.

Eyes (Figure 1a) small, 0.13-0.20 CL, pyriform, corneal diameter 0.45-0.65 X eyestalk length, retinal pigmentation present.

Antennular peduncle (Figure 1b) not reaching beyond scaphocerite, 0.50-0.60 CL; stylocerite length 0.7 X proximal antennular segment length; anterolateral angle of proximal segment acute, reaching to about 0.27 X intermediate segment length; intermediate segment 0.68 X proximal segment length, about 1.8 X distal segment length; all segments with submarginal plumose setae; distal segment fringed laterally and apically with plumose setae.

Antennal peduncle (Figure 1c) about 0.5 X

scaphocerite length; scaphocerite slightly longer than antennular peduncle, 0.70 CL, outer margin straight to slightly concave, asetose, ending in strong subapical spine, length 3.5 X width, proximal lamella and interior margin with plumose setae.

Mandibles without palp; right mandible with about 6 strong, sharp incisor teeth laterally; medially two groups of setae, one group with bent hamate setae, other group with finer straight plumose setae; molar process ridged; left mandible with 6 strong teeth; medially three groups of setae, molar process ridged.

Maxillula with simple palp, slightly expanded distally, with long plumose setae distally, few simple setae proximally; lower lacinia with broadly rounded margin, bearing several rows of plumose and simple setae; upper lacinia broadly elongate, inner edge straight, with several rows of strong spiniform, hamate, denticulate and plumose setae, outer and lower inner margins with plumose setae.

Maxilla with slender tapering palp, shorter than upper endite cleft, setose; margin and submargin of upper and middle endite with simple, hamate, plumose and denticulate setae; lower endite with hamate setae; scaphognathite with regular row of long plumose setae on distal margin, with shorter hamate ones continuing down proximal triangular process which has about eleven long simple setae, some with prominent dilation at base.

First maxilliped with broadly triangular lamellar palp, ending in pointed tip, margins with plumose setae; ultimate and penultimate segments of endites indistinctly divided; inner margin of ultimate segment with long denticulate setae, long rows of plumose, simple and hamate setae submarginally, transverse rows of plumose setae proximally; exopod flagellum distinct, well developed, with submarginal and marginal plumose setae; caridean lobe narrow, with marginal and submarginal plumose setae.

Second maxilliped with dactylar and propodal segments of endopod fused; inner margins of all three proximal segments with long simple, hamate and plumose setae; exopod long, narrow with marginal long plumose setae distally and shorter ones proximally.

Third maxilliped reaching beyond tip of antennular peduncle; endopod three-segmented, basal segment length 7.1 X width, with few hamate setae on distal outer margin; penultimate segment length 8.7 X width, 0.95 X basal segment length, with transverse rows of spiniform hamate setae; distal segment ca. 0.94 X as long as penultimate segment, ending in large claw-like apical hamate seta surrounded by simple and plumose ones, behind which there are 7-9 hamate setae on distal third of posterior margin, clump of serrate and pappose setae proximally; exopod reaching about

0.4 of second endopod segment, distal margin with long plumose setae.

First pereopod (Figure 1d) reaching tip of basal antennular segment; chela length 2.3 X width, movable finger 1.3 X as long as palm, length 3.3 X width; finger tips rounded, without hooks, setal brushes well developed. Carpus attached to chela ventrally, excavated disto-dorsally, length 2.5 X width, 0.91 X chela length, 1.2 X merus length. Merus 0.7 X as wide as carpus. Ischium length 0.48 X merus length. Epipod present.

Second pereopod (Figure 1e) reaching tip of second segment of antennular peduncle, more slender and longer than first pereopod. Chela length 2.4 X width; movable finger length 3.2 X width, 1.5 X as long as palm; finger tips without hooks, setal brushes well developed. Carpus slightly excavated distally, length 5.3 X width, 1.3 X chela length, 1.2 X merus length. Ischium length 0.52 X merus length. Epipod present.

Third pereopod (Figure 1i) over-reaching antennular peduncle tip by about 0.33 distal propodus. Dactylus length 3.1–4.2 X width, ending in prominent claw-like hamate seta surrounded by simple setae, behind which posterior margin bears 4–7 shorter spiniform hamate setae. Propodus length 14.0–14.6 X width, 3.0–3.7 X dactylus length, posterior margin and lateral surface bearing two rows of small spiniform hamate setae. Carpus length 0.7 X propodus length, distal projection feebly developed, posterior and lateral surfaces with up to 5 small hamate setae. Merus 1.7–2.2 X length of carpus, with 1–3 strong, movable spiniform hamate setae along posterior margin. Ischium 0.2–0.3 X length of merus. Epipod present.

Fourth pereopod reaching tip of second segment to tip of third segment of antennular peduncle, morphology similar to third pereopod. Dactylus length 3.5 X width, ending in prominent claw-like hamate seta and 4–7 shorter spiniform hamate setae along posterior margin. Propodus length 14.0 X width, 4.5 X length of dactylus, bearing two rows of hamate setae along posterior and lateral surfaces. Carpus 0.7 X length of propodus, with up to 7 small hamate setae along posterior and lateral surfaces. Merus about 2.1 X length of carpus, with 3–4 spiniform hamate setae on postero-lateral margin. Ischium 0.25 X length of merus. Epipod present.

Fifth pereopod (Figure 1f) reaching tip of second segment to tip of third segment of antennular peduncle. Dactylus length 4.3 X width, ending in claw-like apical hamate seta, bearing comb-like row of 35–45 hamate setae on posterior margin. Propodus length 15.7 X width, 3.0 X dactylus length, bearing two rows of 15–20 short hamate setae on posterior margin. Carpus length 0.5–0.6 X propodus length, bearing 2–6 short hamate setae, distal projection well developed. Merus distinctly

shorter (0.8) but broader (1.3) than propodus, bearing 2–4 large spiniform hamate setae. Ischium about 0.4–0.5 X length of merus, with simple setae. Epipod absent.

Abdomen (1a) well developed, rotund, glabrous, 2.1 CL; sixth abdominal segment 0.47–0.67 CL, length 1.9–2.3 X depth. Second abdominal somite depth (from top of tergum to ventral margin of pleura) about 0.96 CL in fully developed non-ovigerous female, about 0.80 in males and juvenile females.

First pleopodal endopod (Figure 1h) length in adult male 2.2 X proximal width, 0.27–0.33 X exopod length, ovate, wider proximally, broadly rounded distally, inner margin bearing long plumose setae, outer margin with short plumose setae proximally and longer ones distally. Appendix interna absent.

Second pleopodal endopod length in adult male about 0.90 X exopod length, inner border near base with long marginal and submarginal hamate setae. Appendix interna reaching beyond middle of appendix masculina, with many retinaculae distally. Appendix masculina subcylindrical, long hamate setae distally and on inner lateral margin.

Telson (Figure 1g) 0.4–0.5 CL, equal to or just shorter than sixth abdominal segment, tapering posteriorly, ending in rounded margin, dorsal surface with 3–5 pairs of short hamate setae. Posterior margin rounded, with 8–10 spine-like setae, one or two outer-most pairs much shorter than adjacent, somewhat sigmoid, inner pair which in turn is generally thicker and longer than its adjacent inner ones. Uropods distinctly longer than telson; diaeresis on exopod with 8–10 small hamate setae.

Etymology

The specific epithet refers to the habitat from where the species was collected (Latin: *spelunca* = cave). It is used as a noun in apposition.

DISCUSSION

Caridina spelunca sp. nov. is the first in the genus to be described from Western Australia. Its habitat and sympatric fauna have been described by Humphreys (1995). It somewhat resembles *Caridina weberi* De Man 1892 (which is a wide ranging Indo-Pacific species but not yet reported from Australia) in rostral structure but can be easily distinguished from this and other morphologically similar species on the basis of a combination of the following characters in *C. spelunca*: absence of a median spine on the posterior telsonic margin; posterior telson margin with fewer and shorter intermediate setae, each lacking septum and annulus; carpus of first pereopod longer and not deeply excavated and the absence of an appendix interna on the endopod

of the first male pleopod. Of the atyid shrimps currently known from Australia, *C. spelunca* is morphologically most similar to *C. thermophila* which is known from an artesian bore in central Queensland (Riek 1953). However, *C. thermophila* possesses more ventral rostral teeth (4–6), more spiniform setae (8–11) on the dactylus of the third and fourth pereopods and more hamate setae (15–17) on the diaeresis of the uropodal exopod.

ACKNOWLEDGEMENTS

John Short (Queensland Museum, Brisbane) brought the Western Australian atyids to my attention. Specimens, collection data and habitat information were kindly provided by Drs W.F. Humphreys (WAM) and W.F. Ponder (AM).

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Manuscript received 22 January 1996; accepted 28 May 1996.

New records of reef and shore fishes from northwestern Australia

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The fish fauna of reefs and shoals on the outer edge of Australia's North-West Shelf was summarised by Allen and Russell (1986) and Allen (1993). They reported 833 species, mainly from Rowley Shoals, Scott-Seringapatam Reefs, Ashmore Reef, and Cartier Island. Hutchins et al (1995) recorded 45 additional species from the area. The present paper reports 49 new records of reef and shore fishes for Western Australia, including 15 that are new to Australian seas. The fishes were collected or observed by the author on three expeditions between 1991 and 1994. The first of these involved a survey of coastal localities and offshore islands in the Kimberley region between Wyndham and Broome for 17 days in August 1991. A second trip of 19 days duration visited the Monte Bello Islands in August 1993. The final trip, in September 1994, made collections and observations at offshore reefs including Scott, Seringapatam, Ashmore, Hibernia, and Cartier, as well as Cassini Island on the Kimberley coast.

Collections were obtained with a chemical ichthyocide (rotenone powder) and a small multi-prong hand spear. In addition, a series of visual

transects were conducted with the use of SCUBA. Underwater photographs, now deposited in the files of the Western Australian Museum (WAM), were taken of many species and form the basis of several of the records listed below.

The list of new records for Western Australia is presented below. An additional list includes species that were collected for the first time on reefs and islands along the Kimberley Coast, although they are known from offshore sites such as Rowley Shoals and Ashmore Reef. The approximate latitude and longitude for the various localities mentioned in these lists are indicated in Table 1.

Three species, also obtained in these collections, are not included in the present list. They represent new taxa and have been described elsewhere: *Pseudochromis howsoni* Allen (1994a), a pseudochromid from Ashmore Reef; *Amblyglyphidodon batunai* Allen (1994b), a pomacentrid observed at Churchill Reef, and *Cirrhitilabrus randalli* Allen (1995) from Rowley Shoals, Scott-Seringapatam Reefs, Ashmore Reef, and Cartier Reef.

Two additional new taxa, *Gymnothorax* sp. (Kimberley coastal islands) and *Notograptus* sp. (Montgomery Reef and Scorpion Island, Kimberley coast), were also collected. They will eventually be described by the author. An undescribed species of *Opistognathus* was observed at Hibernia Reef. It is widespread in Indonesia (see Kuiter 1992: 144, for illustrations).

ACKNOWLEDGEMENTS

The 1991 Kimberley coast fieldwork was supported by the National Estate Program, an Australian Commonwealth financed grants scheme administered by the Australian Heritage Commission (Federal Government) and the Western Australian Heritage Committee (State Government). Additional funds for the 1991 work were provided by the Australian Geographic Pty Ltd and Mr Harry Butler, Honorary Associate of the Western Australian Museum. The survey of the Monte Bellos Islands in 1993 was part of an Ocean Rescue 2000 Project, funded by the Western Australian Government through the Western Australian Department of Conservation and Land

Table 1 Locality data for new fish records from Western Australia.

Location	Latitude and Longitude
Scott Reef	14°02'S, 121°52'E
Seringapatam Reef	13°38'S, 122°01'E
Ashmore Reef	12°11'S, 123°07'E
Cartier Reef	12°32'S, 123°33'E
Hibernia Reef	11°58'S, 123°21'E
Monte Bello Islands	20°25'S, 115°30'E
Powerful Island	16°05'S, 123°27'E
Lord & Byron Islands	16°10'S, 123°28'E
Beagle Reef	15°21'S, 123°32'E
Churchill Reef	15°31'S, 123°17'E
Prince Regent River	15°37'S, 125°18'E
Rob Roy Reef	14°25'S, 124°51'E
West Montalivet Island	14°17'S, 125°13'E
near Cleghorn Island	14°22'S, 125°25'E
near Descartes Island	14°11'S, 125°38'E
near Fenelon Island	14°09'S, 125°39'E
Cassini Island	13°56'S, 125°37'E
Long Reef	13°48'S, 125°47'E
Scorpion Island	13°52'S, 126°36'E
Tranquil Bay	13°56'S, 127°18'E
King George River	14°03'S, 127°20'E

Management. The 1994 expedition to offshore reefs and the Kimberley coast was partially financed by the Western Australian Museum. The Australian Nature Conservation Agency provided a research permit to conduct surveys at Ashmore Reef. Collecting assistance was provided by Paddy Berry and Clay Bryce of WAM and by Bonnie and Hugh Morrison of Perth Diving Academy. Douglass Hoese (Australian Museum, Sydney) and Helen Larson (Museum and Art Gallery of the Northern Territory, Darwin) assisted with gobiid identifications.

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- List of New Records for Western Australia**
 Key to symbols:
 WAM = Western Australian Museum registration number
 P = photographed only
 V = visual record, no photograph
 * = new record for Australia
- Chlopsidae**
Kaupichthys atronassus Schultz, 1953. Scott Reef (WAM P.30835-059)
- Muraenidae**
Gymnothorax pseudothryssoides (Bleeker, 1852). Powerful Island, Kimberley coast (WAM P.30320-024).
Rhinomuraena quaesita Garmann, 1888. Ashmore Reef (V).
- Ophichthidae**
 **Ophichthus evermanni* Jordan and Richardson, 1908. Powerful Island, Kimberley coast (WAM P.30320-024).
- Clupeidae**
Spratelloides delicatulus (Bennett, 1832). Monte Bello Islands and Beagle Reef, Kimberley coast (WAM P.30680.014 and P.30316-016).
- Bythitidae**
Dinematchichthys ilucoetoides Bleeker, 1855. Long Reef, Kimberley coast (WAM P.30308-001).
- Hemiramphidae**
Zenarchopterus gilli Smith, 1945. King George River and Sunday I., Kimberley coast (C).
- Atherinidae**
Atherinomorus lacunosa (Forster, 1801). Scorpion Island, Kimberley Coast (WAM P.30305-004).
- Syngnathidae**
 * *Doryrhamphus multiannulatus* (Regan, 1903). Monte Bello Islands (P).
 **Phoxocampus belcheri* (Kaup, 1856). Monte Bello Islands (WAM P.30680-021).
- Serranidae**
Cephalopholis cyanostigma (Kuhl and Van Hasselt, 1828). Widespread Kimberley coast (WAM P.30308-015).
- Apogonidae**
 **Apogon fleurieu* (Lacepede, 1801). Ashmore Reef (V).
Apogon lateralis Valenciennes, 1832. King George River, Kimberley coast (WAM P.30300-003).
 **Apogon gilberti* (Jordan and Seale, 1905). Seringapatam Reef (P).
Apogon notatus (Houttuyn, 1782). Ashmore Reef (P).
 **Apogon perlitis* Fraser and Lachner, 1985. Seringapatam and Cartier reefs (P).
 **Gymnapogon philippinus* (Herre, 1939). Montgomery Reef (WAM P.30851-013).
- Lutjanidae**
Lutjanus johnii (Bloch, 1792). Hunter and Prince Regent rivers, Kimberley coast (P).
- Chaetodontidae**
 **Chaetodon decussatus* Cuvier, 1831. Ashmore Reef (P).
Heniochus monoceros Cuvier, 1831. Scott and Cartier reefs (V).
- Pomacanthidae**
 **Chaetodontoplus mesoleucus* (Bloch, 1787). Widespread Kimberley coast (WAM P.30310-001).
- Pomacentridae**
 **Chromis caudalis* Randall, 1988. Ashmore Reef (V).
Pomacentrus littoralis Cuvier, 1830. Monte Bello

Islands and widespread Kimberley coast (WAM P.30302–011, P.30303–012, and P.30316–013).

Labridae

Bodianus anthioides (Bennett, 1831). Seringapatam and Cartier reefs (V).

Coris dorsomacula Fowler, 1908. Ashmore Reef (V).

Diproctacanthus xanthurus (Bleeker, 1856). Widespread Kimberley coast (WAM P.30311–028).

**Halichoeres purpurascens* (Bloch and Schneider, 1801). West Montalivet Island, Kimberley coast (V).

**Paracheilinus mccoskeri* Randall and Harmelin-Vivien, 1977. Scott and Ashmore reefs (WAM P.30836–007).

Trichonotidae

Trichonotus elegans Shimada and Yoshino, 1984. Cartier Reef (WAM P.30881–001).

Pinguipedidae

Parapercis snyderi Jordan & Starks, 1905. Long Reef, Kimberley coast and Monte Bello Islands (WAM P.30307–021, P.30312–018, and P.30690–006).

Blenniidae

Ecsenius lividinalis Chapman and Schultz, 1952. Near Fenelon Island and near Descartes Island, Kimberley coast (WAM P.30311–031).

**Ecsenius namiyei* (Jordan and Evermann, 1903). Ashmore Reef (WAM P.30960–010).

Callionymidae

Synchiropus ocellatus (Pallas, 1770). Scott Reef (WAM P.30834–037).

Gobiidae

Amblyeleotris gymnocephalus (Bleeker, 1853). Near Cleghorn Island, Kimberley coast (P).

Amoya madraspatensis (Day, 1868). Tranquil Bay, Kimberley coast (WAM P.30301–006).

Cryptocentrus insignitus (Whitley, 1956). Lord and Byron Islands, Kimberley coast (WAM P.30319–026).

**Ctenogobius tangaroai* Lubbock and Polunin, 1977. Scott Reef (WAM P.30835–013).

Drombus triangularis (Weber, 1911). Mission Bay, Kimberley coast (WAM P.30303–014).

Eviota sebreei Jordan and Seale, 1906. Near Fenelon Island and near Descartes Island, Kimberley coast (WAM P.30310–010 and P.30311–008).

Favonigobius melanobranchus (Fowler, 1934). Mission Bay, Kimberley coast (WAM P.30849–033).

**Oplopomops* sp. (Peters, 1855). Seringapatam Reef (WAM P.30883–002).

Trimma taylori Lobel, 1979. Seringapatam Reef (WAM P.30839–001).

Trimmatom macropodus Winterbottom, 1989. Hibernia Reef (WAM P.30844–037).

Trimmatom zapotes Winterbottom, 1989. Scott Reef (WAM P.30835–004).

Microdesmidae

Parioglossus palustris (Herre, 1945). Lord and Byron Islands, Kimberley coast (WAM P.30319–024).

Parioglossus philippinus (Herre, 1945). King George River, Cassini Island, and near Descartes Island, Kimberley coast (WAM P.30300–005, P.30309–013, and P.30311–034).

Acanthuridae

Naso annulatus (Quoy and Gaimard, 1825). Scott, Hibernia, and Cartier reefs (V).

Naso thorpei Smith, 1966. Cartier Reef (V).

Naso thynnoides (Valenciennes, 1835). Cartier Reef (V).

List of fishes previously recorded from offshore reefs in Western Australia, but recorded for the first time from coastal localities

Muraenidae

Uropterygius concolor Ruppell, 1838. Cassini Island, Kimberley coast (WAM P.30309–004).

Holocentridae

Sargocentron caudimaculatum (Ruppell, 1838). Rob Roy Reef, Kimberley coast (V).

Serranidae

Epinephelus ongus (Bloch, 1790). Near Descartes Island, Kimberley coast (V).

Pseudochromidae

Labracinus cyclophthalma (Muller and Troschel, 1849). Ashmore Reef, Timor Sea and Cassini Island, Kimberley coast (WAM P.30847–003).

Lutjanidae

Macolor niger (Forsskal, 1775). West Montalivet Island, Kimberley coast (V).

Caesionidae

Caesio caerulea Lacepede, 1801. Widespread Kimberley coast (V).

Chaetodontidae

Chaetodon vagabundus Linnaeus, 1758. Cassini, West Montalivet Islands and Rob Roy Reef, Kimberley coast (P).

Pomacentridae

Acanthochromis polyacantha (Bleeker, 1855). Widespread Kimberley coast (WAM P.30305–003, P.30307–005, and P.30308–013).

Pomacentrus adelus Allen, 1991. Widespread Kimberley coast (WAM P.30311–030).

Labridae

Bodianus diana (Lacepede, 1801). Cassini Island, Kimberley coast (V).

Halichoeres hartzfeldi (Bleeker, 1852). Near Fenelon Island and near Cleghorn Island, Kimberley coast (WAM P.30312–006).

Halichoeres melanurus (Bleeker, 1851). Widespread

Kimberley coast (WAM P.30307-025, P.30310-016, P.30311-029, P.30847-004).

Microdesmidae

Ptereleotris microlepis (Bleeker, 1856). Cassini I., near Fenelon Island, and near Cleghorn Island, Kimberley coast (WAM P.30312-017 and P.30847-001).

Siganidae

Siganus vulpinus (Schlegel and Muller, 1845). Cassini Island and Rob Roy Reef, Kimberley coast (P).

Manuscript received 19 May 1995; accepted 7 May 1996.

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Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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Spelling should follow the *Concise Oxford Dictionary*.

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The original and two copies of manuscripts and figures should be submitted to the Editors, c/- Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance an IBM compatible disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. WordPerfect, Wordstar, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

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The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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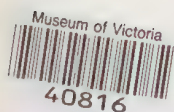
Dates of Publication

Records of the Western Australian Museum

Volume 17, Part 1	26 May 1995
Volume 17, Part 2	27 June 1995
Volume 17, Part 3	20 October 1995
Volume 17, Part 4	21 June 1996



Records of the Western Australian Museum



Volume 18 Part 2 1996

Records of the Western Australian Museum

The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

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Printed and published by the Western Australian Museum
© Western Australian Museum, December 1996
ISSN 0312 3162

Cover: The Nicobar Pigeon, *Caloenas nicobarica*, from Indonesia.
Illustration by Jillian Ruse.

A new species of *Melomys* (Rodentia: Muridae) from Riama Island, Tanimbar Group, Maluku Tenggara, Indonesia

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Abstract – Three specimens of *Melomys* recently collected from Riama Island, Tanimbar group, Maluku Tenggara, are herein described as a new species.

INTRODUCTION

Prior to October 1992, members of the essentially Australo–papuan murid rodent genus *Melomys* Thomas, 1912 were unreported from the islands of the southern Maluku Administrative Province of Indonesia. Since that date, terrestrial vertebrate surveys of this region by staff from the Western Australian Museum and the Museum Zoologicum Bogoriense have collected *Melomys rufescens* (Alston, 1877) and *M. cf. levipes* (Thomas, 1897) from Aru Island; *M. bannisteri* Kitchener and Maryanto, 1993 from Kai Besar Island and *M. cooperae* Kitchener, 1995 from Yamdena Island (Tanimbar Group).

A recent visit to Riama Island (Pulau Riama), a small islet approximately 6 km from the west coast of Salaru Island in the Tanimbar group of islands (Figure 1), resulted in the collection of three specimens of *Melomys*. This paper describes these specimens as a new species.

METHODS

Two of the Riama Island specimens were collected by D.J. Kitchener by hand. A third specimen was purchased from fishermen on that island. This latter specimen was infested with maggots; its skull was removed and cleaned at Saumlaki, Yamdena Island, but its carcass was disposed of by accident by hotel staff after its sex was determined.

The two freshly collected specimens were weighed in the field prior to their fixation with formalin. External measurements were recorded from these two specimens following their fixation. All measurement (in mm) were taken with digital callipers: externals to 0.1 mm; skull and dental to 0.01 mm. Measurement points follow Tate (1951). Pelage and colour descriptions were determined from the colour charts of Smithe (1975). Scale number per cm was averaged from six measurements recorded from the mid part of the tail.

Adult condition was judged from reproductive status because as noted in Kitchener and Maryanto (1995) basicranial sutures were clearly visible in specimens of *Melomys cooperae* from Yamdena Island that were reproductively mature and had very worn teeth. This was also the situation with the two female *Melomys* from Riama Island.

TAXONOMY

Melomys howi Kitchener sp. nov.

Figures 1–3, Table 1

Holotype

Museum Zoologicum Bogoriense specimen number 15912 (field number WAM M44753); adult (pregnant) female; weight 73 gm; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; collected by hand on 11 November 1994 by D.J. Kitchener.

Paratypes

Western Australian Museum number WAM M44754, adult (recently parturient) female, weight 61 gm; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate. Collected by hand on 11 November 1994 by D.J. Kitchener. WAM M44755, old adult male with very worn teeth; skull only. Purchased on 12 November 1994. From same locality as holotype.

Type Locality

Riama Island (Pulau Riama); Tanimbar Group; Maluku Tenggara, Indonesia (8°09'S, 130°53'E); at sea level; on white sand 30 metres from coast in an open moderately high (to 2 metre) shrubland.

Diagnosis

Melomys howi differs from all other species of *Melomys* by having the following combination of characters: small body and skull size; white abdominal fur; three hairs per tail scale; tail scales flat and not sculptured; 11–13 scales per cm in mid section of tail; bicoloured tail; broad feet; narrow

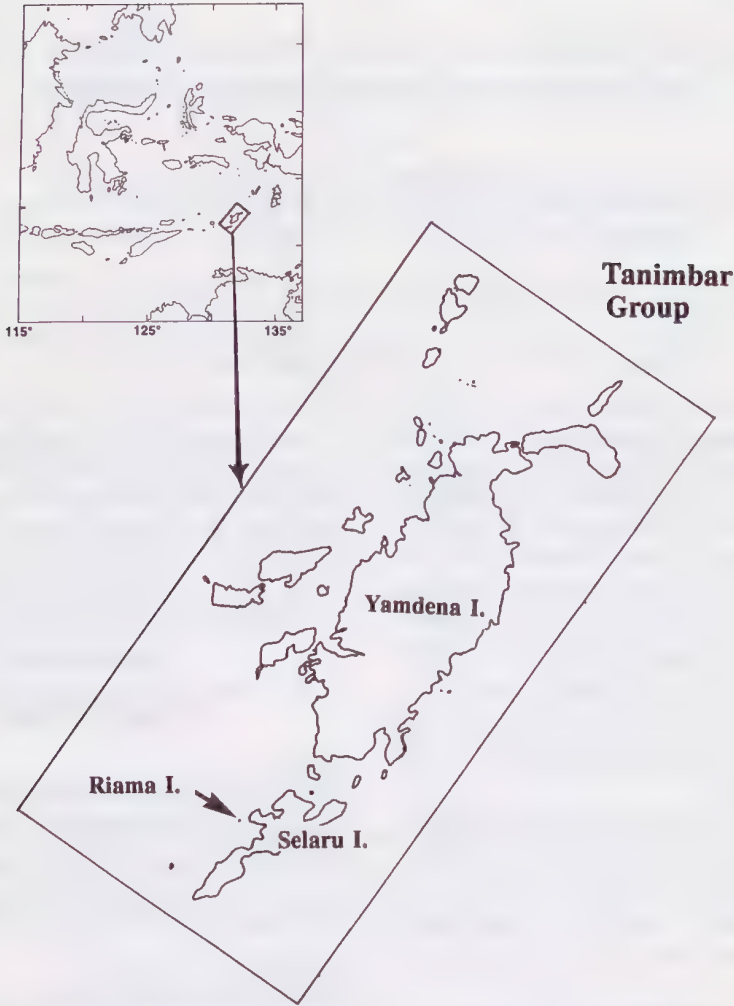


Figure 1 Map showing the locality of Riama Island and the Tanimbar groups of islands.

interorbital region; M^1 and M^2 with well developed posterior cingulum with central vestigial cusplet; unreduced M^3 ; and long incisive foramen.

Description

Measurements of skull, dentition and externals are presented in Table 1.

Skull (Figure 2)

Skull small: greatest skull length 31.2–34.0 and zygomatic width 16.2–16.3, with a narrow rostrum. Skull dorsal profile sharply curved from nasal distal tip to anterior part of frontal when it slopes gently downward to mid parietal region and then more sharply downwards to the posteriormost edge of skull; interparietal wide (8.8–9.1); parietal moderately inflated; frontal anterior part forms a

slight median sulcus that reaches to posterior one-quarter of nasal; nasal moderately long (11.3–12.3), constricted proximally and flared to a breadth of 3.8–4.2 distally; anterior edge of premaxilla flange projected dorsally above incisor, almost vertical or slightly convex leading edge – nasal projects to a point approximately above or slightly anterior to this leading edge; zygomatic arch moderately thickened; zygomatic plate broad (4.3–4.9), anterodorsal part of leading edge projects furthest anteriorly from which point it curves gently posteriorly; infraorbital fissure moderately wide; lachrymal bones elongate, project only slightly outside curve of orbit edge; postsquamosal hook well developed, forms a slight vertical ridge with lateral occipital and mastoid – this ridge does not progress to interparietal posterior margin;

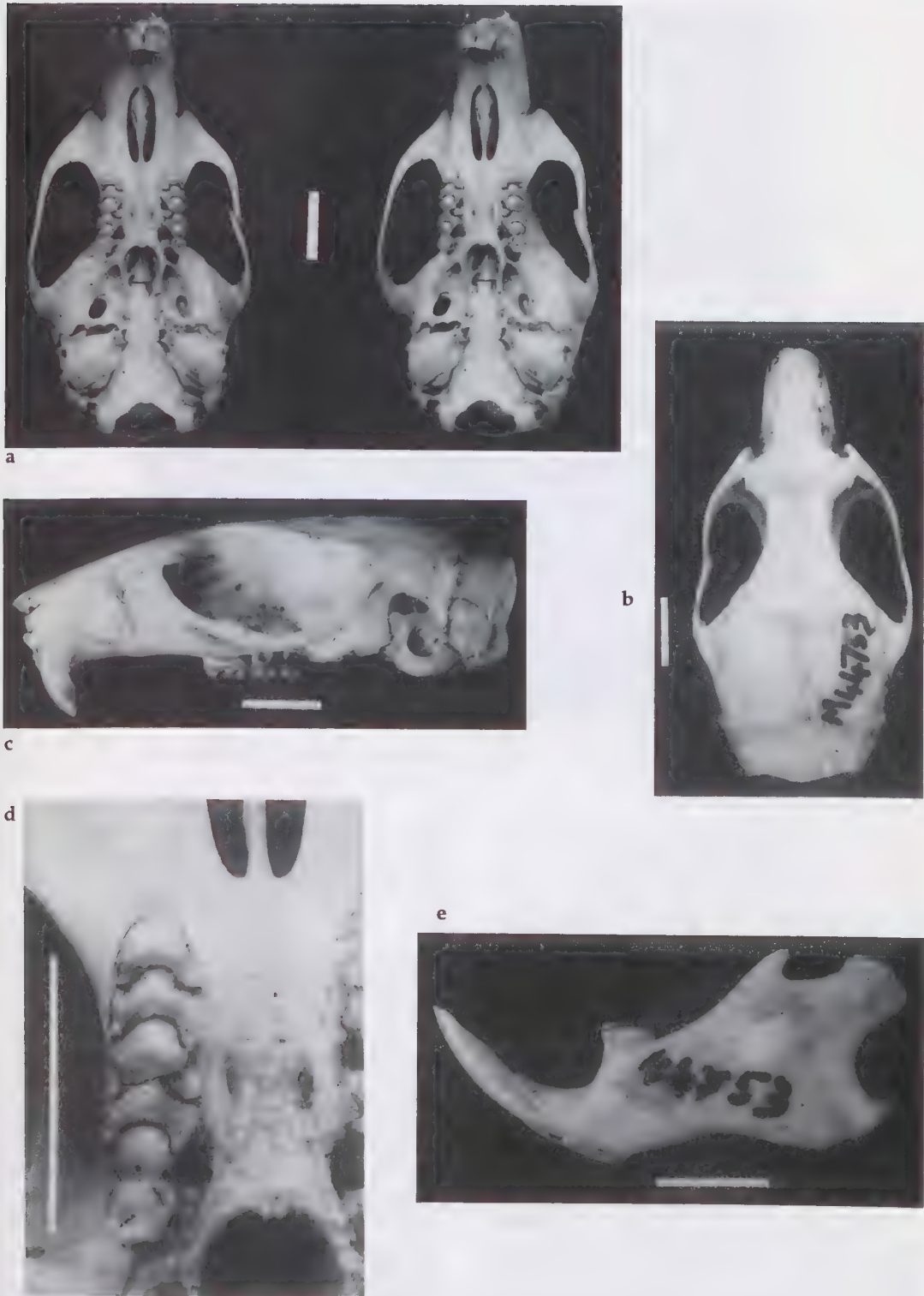


Figure 2 Skull, a, ventral view (stereopair), b, dorsal view, c, lateral view; d, right upper molar row; e, dentary. Scale 5 mm.

Table 1 Measurements (in mm) of the skull, dentition and external body and weight of *Melomys howi* holotype and paratypes.

CHARACTER	Holotype MZB15912	WAM M44754	WAM M44755
Sex	♀	♀	♂
Greatest skull length	32.19	31.17	33.93
Condylolincisor length	29.91	28.60	31.73
Zygomatic width	16.16	16.29	—
Interorbital breadth	4.61	4.90	4.96
Interparietal breadth	8.76	9.12	9.07
Braincase breadth	12.87	13.56	—
Mastoid width	11.44	11.63	—
Nasal length	12.25	11.29	12.10
Nasal breadth	4.00	3.78	4.22
Zygomatic plate breadth	4.37	4.34	4.90
Diastema length	8.42	7.59	9.56
Height muzzle (behind ant. pal. for.)	8.10	8.05	8.66
Palatal length	16.29	15.16	17.21
Ant. palatal foramen length	5.56	4.84	5.95
Ant. palatal foramen breadth	2.00	2.03	2.13
Mesopterygoid fossa breadth	2.49	2.58	2.71
M ¹ –M ¹ breadth (inside)	2.65	2.53	2.57
Bulla length	4.72	4.60	4.59
M ¹ –M ³ crown length	6.02	6.11	5.98
M ¹ –M ³ alveoli length	6.14	6.37	6.42
M ¹ crown length	3.12	3.16	3.02
M ¹ crown breadth	1.79	1.89	1.79
M ² crown length	2.37	2.25	2.13
M ² crown breadth	1.77	1.82	1.80
M ³ crown length	1.25	1.18	1.42
M ³ crown breadth	1.33	1.24	1.33
Dentary length	18.92	18.24	20.14
M ₁ M ₃ (crown) length	6.21	6.07	—
Snout to vent length	112.2	111.5	—
Tail to vent length	135.6	137.2	—
Ear length (from basal notch)	15.5	15.2	—
Pes length (without claw)	27.2	26.0	—
Pes breadth to base of digit V	7.7	7.2	—
Tibia length	37.0	32.7	—
Weight (gm)	73	61	—
Scale No./cm	12.2 ± 0.8	12.7 ± 0.7	—

postglenoid foramen large, projects dorsally to form crescent shape; temporal ridges faint, immediately anterior to frontal/parietal suture; rostrum posterolateral swelling only slightly inflated; anterior palatal foramen long (4.8–6.0) but terminate posteriorly anterior of M¹ anterior alveolus, slightly bowed outwards; palate narrow, posterior part highly fenestrated, terminating posteriorly at a point level with anterior part of M³; mesopterygoid and parapterygoid fossae narrow; foramen ovale ventral fossa large; bulla moderately long (4.6–4.7), moderately inflated, with short and robust eustachian process.

Dentition (Figure 2)

Molars moderately large, M³ cusp very long for *Melomys* (see Menzies 1990, Figure 3), M³ cusp length 20–22% length of M^{1–3} cusp length; M¹ anterior and intermediate lamellae with very well developed lingual cusps; posterior lamella without lingual cusp but with spacious posterior cingulum with a central vestigial cusp; M² with moderately large anterolingual cusp only remaining of anterior lamella, intermediate and posterior lamellae well developed – the latter with posterior cingulum and central vestigial cusp as on M¹. M³ with small anterolingual cusp, separate from posterior



Figure 3 Pes plantar surface, a and tail, b, of *Melomys howi* holotype. Scale, 5 mm.

lamella; molar rows diverge posteriorly from each other; upper incisors slightly opisthodont, anterior face orange. First and second lower molars each with well-developed posterior cingulum.

Externals (Figure 3)

Small body size with snout to vent length 112 and weight 61–73 gm. Tail long (136–137) and averaging 121–123% of body length; ears short (15.2–15.5); pes moderately long (26.0–27.2), and wide (7.2–7.7). Scales on tail not raised to form a ridge or hump (Figure 3b). Plantar pads of pes and manus similar to those of *M. bannisteri* from Kai Besar Island but differ from those of *M. cooperae* in that the interdigital pads between digits 2 and 3 do not overlap the interdigit pad between digits 1 and 2 (Figure 3a). There are two pairs of inguinal teats.

Pelage

Dominant colour of dorsal surface pelage tawny, resulting from tawny tipping to the medium neutral gray colour of basal two-thirds of hairs. Head slightly contrastingly coloured: cinnamon

and forehead evenly grading into smoke gray of temporal region, but contrasting with buff yellow of cheeks, small white patch at base of the mystacial vibrissae and dark rings around eyes. Hairs in mid dorsum with length of 15 while those of mid forehead 8; flanks cinnamon tipping to the medium neutral gray of basal two-thirds of hairs. Lips, throat, chest, abdomen to anus, inside of thigh, manus and pes upper surface white; interface between white of abdomen and cinnamon of flanks cream color. Abdomen hairs 10 long; outer leg surface buff yellow. Ear pinna skin antique brown; pinna lightly furred inside and outside with short clay color hairs. Tail skin bicoloured: glaucous dorsally and a pale neutral gray ventrally.

Tail scales with three hairs per scale; tail hairs moderately long (0.8) slightly longer than scale breadth.

On head numerous black mystacial vibrissae up to 45 long; numerous short (up to 10 mm) white submental vibrissae; two short (up to 5) white interramal vibrissae; a single long (up to 18) black genal vibrissa; several long (up to 20) black



Figure 4 Habitat of *Melomys howi* at type locality.

supraorbital vibrissae and 1–3 long (up to 8) white ulnar vibrissae.

Habitat

Pulau Riama is a small flat sandy islet that as recently as 1990 was a noted nesting site for Green and Hawksbill turtles. Since then hunting of turtles on this island by fishermen from nearby Salaru Island has resulted in the virtual absence of turtles nesting on the island. The presence of numerous turtle hunters and fishermen on the island has also led to the disturbance of much of the low dune vegetation fringing the coast. *Melomys howi* favours the open low bushes (Figure 4), particularly beneath the patches of moderately closed stands of 5 m high *Casuarina* trees fringing the coast. A group of 10–15 *M. howi* individuals were observed in an area of about 5 m² for about one hour between 1200 – 1300 hrs feeding on seeds in the leaf litter beneath shrubs.

Reproduction

The female holotype was pregnant with two small fetuses in the left uterine horn. The crown to rump length of these fetuses was approximately 7.4. There were no obvious implantation scars on the right uterine horn.

The other female collected (WAM M44754) had recently given birth; its left uterine horn was only partially involuted, bruised, and had two clear implantation sites. Vestiges of an umbilical cord were apparent in the vagina. No implantation scars were observed in the right uterine horn. The four inguinal teats were slightly enlarged to a length of 1.8 and there was more mammary development than in the pregnant holotype.

Etymology

Named after Dr Richard Alfred How in commemoration of his fiftieth birthday and in acknowledgement of his great contribution to the field work involved in the terrestrial vertebrate faunal survey of eastern Indonesia between May 1988 to September 1993.

Remarks

Melomys howi differs from the other *Melomys* on the Tanimbar Islands (*M. cooperae* Kitchener, 1995) in having three long rather than one short hair per tail scale; considerably smaller cranial dimensions; posterior cingulum of m¹⁻² less well developed and in details of plantar pads.

It differs from the geographically next closest *Melomys* (*M. bannisteri* Kitchener and Maryanto, 1993) from Kai Besar island, Maluku Tenggara, in having three hairs per tail scale; in dental morphology; more inflated bulla; longer incisive foramen which is widest anteriorly rather than posteriorly; tail longer and much longer tail hairs.

It may be superficially confused with some forms of *Melomys lutillus* (Thomas, 1913), a species complex with a New Guinea and Northern Australian distribution. It, however, differs from *M. lutillus* in having larger skull measurements; broader pes; and in having larger scale tails except for the forms *M. l. frigidicola* Tate, 1951, and *M. l. froggatti* Troughton, 1937. It differs from *M. l. frigidicola* in having snout to vent length smaller (111–112 v. 130); bulla shorter (4.6–4.7 v. 4.8); and zygomatic plate much broader (4.3–4.9 v. 3.5). It differs from *M. l. froggatti* in having abdominal fur white and not grey; and a cranium not abruptly rounded anteriorly.

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of Mr Andrew Reeves, Executive Director, Western Australian Museum; and Drs M. Amir, Director, Balitbang Zoologi, LIPI. Thanks also to Mr Jonathon Holmes, Australian Broadcasting Commission, for his companionship on P. Riama. Expedition costs were defrayed by a grant to the senior author from the Australian Nature Conservation Agency.

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Manuscript received 17 January 1996; accepted 7 May 1996.

Status of *Anadara trapezia* (Deshayes) (Bivalvia: Arcoida) from Oyster Harbour, Albany (Western Australia) as compared with east Australian populations

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Abstract – A study of allozymes of the arcoid *Anadara trapezia* was carried out to estimate the degree of divergence associated with the temporal and geographical isolation of the southwestern Australian population from the east Australian population. A survey of electrophoretic variation at 27 putative loci coding for enzymes revealed no evidence of divergence or speciation of the Western Australian population. At all surveyed loci in all sample sets, the same most common alleles were found. Questions are raised regarding the geological time of separation of those populations. Could the time span have been more recent than paleogeological records suggest or is this species made up of a set of well adapted gene complexes that have been stable for thousands of years?

INTRODUCTION

In the marine environment, gene flow is regulated by the rate of exchange of waters between populations. In the absence of such water movement, geographic barriers to gene flow may result in genetic divergence between populations of species with pelagic larval dispersal (Burton 1986; Hedgecock 1986). The degree of divergence and speciation is related to the length of time of separation between populations. The detection of genetic differences or its lack between populations from different regions provides evidence of the isolation or continuity of those populations. Ideally a multidisciplinary approach in the delineation of a species would include data on the geographic distribution, both past and present, morphology, ecology, physiology and biochemistry, reproduction, and genetics (White 1978). However, there is a paucity of cases where all this information has been collated (see Gosling 1994).

Anadara trapezia (Deshayes 1839), a bivalve mollusc of the order Arcoida, is a common species found in hyposaline estuaries from Cairns, northern Queensland (Dixon 1975) to Port Philip Bay, southern Victoria (e.g., Macpherson 1966; Poore and Rainier 1974; Smith, Coleman and Watson 1975; Dixon 1975) and in southern Western Australia at Oyster Harbour near Albany (Kendrick and Wilson 1959). In South Australia, the vast areas of tidal flats and sea grass beds in Gulf St. Vincent are considered suitable habitats for *Anadara trapezia*. However, no live individual has been found in recorded history (e.g., Cotton 1957, 1961; Macpherson and Gabriel 1962; Dixon

1975), despite an attempt to reintroduce *A. trapezia* in Gulf St Vincent in 1956. The eastern and western population can be considered isolated from one another at the present time.

The Quaternary was a period of enormous change. The dramatic changes in climate were accompanied by large fluctuations in sea level, temperature and circulation. These processes resulted in the repeated production and removal of geographic barriers between the populations of temperate eastern and western Australia. Such conditions are believed to favour speciation (Heatwole 1987).

The fossil record shows that the distribution of *A. trapezia* around the Australian coast was more widespread in the past than it is today (Kendrick 1990). In Western Australia, the most northerly published fossil record is Lake McLeod at the mouth of the Lyndon River (Kendrick 1990; Kendrick *et al.* 1991). This is of particular importance as the disappearance of the species from this area provides a good indication of the drying up of rivers and change in the character of estuaries in that region (Kendrick *et al.* 1991). In South Australia during the Late Pleistocene the Glanville Formation was laid down during a period when the water in the region was much warmer than present day conditions and *A. trapezia* flourished (see Ludbrook 1984). *A. trapezia*, together with other molluscs then disappeared from South Australia. Fossils are also found in Tasmania, near Launceston (e.g., Goede *et al.* 1993) and also North Island, New Zealand (e.g., Crozier 1962; Beu and Maxwell 1990; Bryner and Grant-

Mackie 1993, Grant-Mackie and Cook 1990). *A. trapezia* apparently sporadically colonized New Zealand during the Late Pliocene period.

The distribution of *A. trapezia* is now restricted to the eastern coast of Australia with a second, disjunct, southwestern Australian population. Questions have been raised as to whether the southwestern Australian population of *A. trapezia* has diverged during the separation time from the eastern populations. Speciation depends not only upon the spatial duration of the geographic barrier, changes in climate and related fauna and flora but also upon the characteristics of the organism itself. These include habitat selection, vagility and means of reproduction and dispersal. The phenomenon of disjunction has aroused considerable interest in studies of speciation and has been studied in great detail by classical geneticists (e.g., Mayr 1942, 1954, 1963; Huxley 1942). Even though it is generally accepted that geographic isolation favours allopatric speciation, other factors such as special ecological features are also important (e.g., Johnson and Black 1990).

The aim of the study was to determine the level of genetic divergence and hence the specific status

of the geographically disjunct southwestern Australian population of *A. trapezia* relative to the east Australian populations.

MATERIALS AND METHODS

Seven individuals of *Anadara trapezia* were obtained from Oyster Harbour, near Albany, Western Australia. To examine the degree of genetic divergence in this population, the sample set from Oyster Harbour (35°30'S, 118°E) was compared with two sample sets, each of seven specimens, one from Corinella, Western Port Bay Victoria (38°22'S and 145°34'E), and the other from Fingal Bay, Tweed Heads estuary, northern New South Wales (28°16'S and 153°35'E). These two samples were taken as representatives of the southern and northern sections of the east coast population respectively.

As discussed in Richardson *et al.* (1986), the sample size needed for the electrophoretic detection of a suspected cryptic species is a minimum of five individuals. Since the detection of cryptic species relies heavily upon finding fixed differences, the method depends upon the number

Table 1 Electrophoretic conditions and staining methods. * Indicates polymorphic locus. Locus was considered polymorphic if more than one allele was detected.

Enzyme	Abbreviation	E.C. Number	Buffer system	Number of loci
Alanopine dehydrogenase	ALPD*	1.5.1.17	A	1
Enolase	ENOL	4.2.1.11	B	1
Glutamate dehydrogenase	GDH	1.4.1.3	A	1
Isocitrate dehydrogenase	IDH*	1.1.1.42	B	1
Glucose-6-phosphate dehydrogenase	G6PD	1.1.1.49	A	1
Sorbitol dehydrogenase	SORDH	1.1.1.14	A	1
Glucose dehydrogenase	GLDH	1.1.1.118	A	1
6-phospho gluconate dehydrogenase	6-PGD	1.1.1.44	A	1
Malic enzyme	ME*	1.1.1.40	A	1
Fumarate hydratase	FUM	4.2.1.2	A	1
Strombine dehydrogenase	STR	1.5.1.X	A	1
Aconitate hydratase	ACON	4.2.1.3	A	1
Esterase methylumbelliferyl butyrate	EST	3.1.1.1	B	1
Alanine amino transferase	GPT 1	2.6.1.2	B	2
	GPT 2			
Malate dehydrogenase	MDH 1*	1.1.1.37	A	2
	MDH 2*			
Octopine dehydrogenase	ODH*	1.5.1.11	A	1
Cytosol amino peptidase/leucine amino peptidase	CAP*	3.4.11.1	A	1
	Formerly LAP*			
Mannose phosphate isomerase	MPI*	5.3.1.8	C	1
Phosphoglucomutase	PGM*	2.7.5.1	A	1
Glucose phosphate isomerase	GPI*	5.3.1.9	A	1
Arginine kinase	AK	2.7.3.3	A	1
Aspartate amino transferase	GOT 1	2.6.1.1	A	2
	GOT 2			
Pyruvate kinase	PYR	2.7.1.40	B	1
Guanine deaminase	GDA*	3.5.4.3	D	1

Table 2 Allelic profile of 21 individuals at 27 electrophoretic putative enzyme loci.
Key: 1 indicates presence, 0 indicates absence of allele. Alleles named alphabetically and putative enzyme loci numbered in order of increasing anodal mobility.

		Individuals																				
		Western Australia							Victoria							Northern New South Wales						
Loci	Alleles	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
ALPD	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	B	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0
ENOL	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GDH	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
IDH	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	B	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
G6PD	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SORDH	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GLDH	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6PGD	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ME	A	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	B	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
FUM	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
STRDH	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ACON	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
EST	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GPT1	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GPT2	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
MDH1	A	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	B	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0
MDH2	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	B	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0
	C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
ODH	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	B	1	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1	0	1	0	1
	C	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	1
CAP	A	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	B	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	1	0
	C	1	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
MPI	D	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	A	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
	B	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1
	C	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1	1
	D	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0
	E	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
PGM	F	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
	C	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
	D	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	1	1	1
	E	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1
GPI	F	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	A	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1
	B	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0
ARK	C	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
GOT1	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GOT2	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PYR	A	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
GDA	A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1

of loci screened rather than on the number of individuals surveyed. Seven animals from each locality were used as this was the maximum number that could be run on a single gel, which is necessary if mobilities are to be compared.

Twenty seven putative enzyme loci including 11 polymorphic enzymes were surveyed using cellulose acetate electrophoresis (Cellogel, Chemtron, Italy). The enzymes studied are detailed in Table 1.

Recipes for staining these enzymes can be found in Richardson *et al.* (1986) and Manchenko (1994). Four buffer systems were used (A) 0.05 M Tris-Maleate-EDTA-MgCl₂ pH 7.8, (B) 0.01 M Citrate-phosphate pH 6.4, (C) 0.025 M Tris-glycine-MgCl₂ pH 8.5, (D) 0.05 M Tris-maleate pH 7.8 (see Richardson *et al.* 1986 for details).

All 21 specimens were run on a single gel and mobilities compared. At each locus, putative alleles were labelled alphabetically in order of increasing electrophoretic mobility of their corresponding electromorphs. Allelic differentiation was quantified using pair-wise comparison within sample sets and among sample sets by the sum of similarities (0, different mobility, 1 same mobility). As the data is approximately normally distributed, the mean and standard error of all observations within and among regions were calculated to evaluate the level of divergence and, hence, species status. This simple statistic was used as the presence of null alleles at many loci (Yardin

unpublished) made any more complex analyses invalid.

RESULTS

The allelic profile of each individual is summarised in Table 2. Pair-wise comparisons at all loci were calculated and the results are tabulated in matrix form (Table 3). The means and standard deviation of similarities within and between localities are shown in Table 4. Because the values are not independent, simple parametric tests of similarity cannot be used.

It is clear that the same suite of allelomorphs occur in all three population sets (Table 2) and that there is no greater differentiation between individuals from the same population than there is between individuals from different populations. Western Australian individuals shared 24.81 alleles on average while the average number of alleles they shared with Victoria and northern New South Wales were 24.69 and 25.41 respectively. There is no evidence of any divergence between the populations and therefore no evidence of speciation.

DISCUSSION

The electrophoretic comparisons within and among the three populations of *A. trapezia* did not provide any evidence of genetic divergence in this

Table 3 Pair-wise comparison of individuals showing commonality of alleles within and among populations.

		Western Australia							Victoria							Northern New South Wales						
		1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
WA	1	-																				
	2	26	-																			
	3	28	26	-																		
	4	24	23	24	-																	
	5	24	23	23	23	-																
	6	23	23	23	23	28	-															
	7	26	26	27	26	26	26	-														
VIC	1	25	25	25	25	25	25	28	-													
	2	25	25	24	24	23	23	26	26	-												
	3	24	25	23	23	25	25	26	27	25	-											
	4	27	25	26	23	24	22	25	25	26	24	-										
	5	27	26	27	24	24	24	27	28	26	26	28	-									
	6	24	24	24	25	23	23	26	27	25	24	24	26	-								
	7	24	24	24	24	24	24	27	26	24	24	25	27	28	-							
Northern NSW	1	25	23	24	25	22	22	25	24	24	23	24	24	23	23	-						
	2	27	25	26	25	22	22	25	24	24	24	27	27	24	25	27	-					
	3	26	26	28	26	25	25	29	27	26	25	26	28	25	26	26	26	-				
	4	27	26	27	26	25	25	28	27	27	25	26	28	27	26	27	27	28	-			
	5	27	27	27	25	25	25	28	28	26	25	26	28	27	26	24	26	27	28	-		
	6	26	25	26	27	24	24	26	27	25	24	25	26	27	25	25	26	26	28	28	-	
	7	26	26	27	24	23	23	27	25	25	24	26	26	24	24	25	26	28	27	26	26	-

Table 4 Statistical description of pair-wise comparisons of allelic similarities within and between populations

	WA/ WA	VIC/ VIC	NSW/ NSW	WA/ VIC	WA/ NSW	VIC/ NSW
Mean	24.81	25.76	26.52	24.69	25.41	25.47
Standard error	0.39	0.30	0.24	0.19	0.24	0.20

species. Moreover, populations that have been isolated for considerable time usually show some degree of divergence, at least in allozymes (Richardson *et al.* 1986) and the lack of any evidence of divergence for populations that have presumably been separated for at least 10,000 years is very surprising.

The results obtained give rise to several hypotheses. It is possible that (1) the population in Albany has been recently introduced rather than the remains of a relict of the Western Australian population seen in the fossil record. Cotton (1957,1961) reported an unsuccessful attempt to reintroduce *A. trapezia* to St Vincents' Gulf in South Australia. While no evidence is known for such an attempt in Western Australia, the limited distribution of the species does leave such a possibility open. Alternatively, a set of well adapted gene complexes exists in the species resulting in very slow rates of evolution.

(2) If the observed allozyme variation is adaptive, rather than selectively neutral (Kimura and Ohta 1973) then, as long as the environment at Oyster Harbour is similar to those of *A. trapezia* habitats in eastern Australia, then there is no ground for expecting changes in the genotypes.

(3) The evolutionary literature is full of discussion of issues related to the rate of evolution. Is it gradual (e.g., Wright 1931; Ayala *et al.* 1975; Provine 1986; Wake, Yanev and Freelow 1989) or is it punctuated (Eldredge and Gould 1972; Stanley 1975). It has been much debated that most well-established species evolve at a very slow rate (e.g., Mayr 1982; Grant 1963; Barton and Charlesworth 1984). Mayr (1982) relates this to what he termed "the unity of the genotype" i.e., individuals within a species carry within their genetic make-up a well-integrated set of adapted genes (Dobzhansky 1951). Restructuring of the genotype is less likely to happen in large populations as gene flow will tend to counteract the effect of mutations in a stable environment. Isolated and small populations are thus most vulnerable to adaptive and selective changes. However most isolated populations either reestablish contact with the parent population or become extinct. Mayr (1982), while acknowledging that evolutionary events such as speciation are usually linked with swift dramatic changes in environmental conditions, i.e., changes in the adaptive landscape, identified two different aspects of allopatric speciation. Firstly, widely

discontinuous portions of a species often fail to diverge, and secondly, highly isolated populations are sometimes very drastically different from the parent population. Thus, it appears that every founder population does not speciate. Moreover, homeostatic mechanisms prevent well established species from undergoing rapid evolutionary change. As Carson (1975) pointed out, "the loosening up of the cohesion of the genotype is an important and perhaps the decisive component in much of speciation".

(4). Alternatively, Eldredge and Gould (1972) and Gould and Eldredge (1977) proposed the concept of punctuated equilibrium. This concept postulates that evolution does not happen gradually but rather, it appears that large wide-ranging species remain static for a very long time and new forms arise in peripheral small isolated populations at a very rapid rate. However the influences of founder events on the magnitude and pattern of speciation are in theory directly related to the size and duration of such events and also on the resulting rate of population recovery (Nei, Maruyama and Chakraborty 1975). In addition, as discussed by Avise (1994), the survival of particular lineages following a bottleneck may be a purely stochastic event.

In the eastern regions of Australia *A. trapezia* has survived for a relatively long time in most estuaries even though it may have undergone drastic population crashes in various places in periods due to catastrophes such as major floods. Recolonisations have been observed in some places on the east coast due to the ability of the organism to disperse by pelagic larvae and also the presence of ocean currents that enable connectedness among geographically separated populations. The population in Oyster Harbour, near Albany, however requires special management strategies as there are no adjacent populations to replenish the genetic pool in the event of a major catastrophe. Indiscriminate exploitation by commercial fishers may also result in the extinction of this species from the southwestern region of Australia.

ACKNOWLEDGEMENTS

We wish to thank Shirley Slack-Smith (Western Australia Museum) and Anthony Forster (Fisheries Department of Western Australia) for providing specimens of *A. trapezia* from Oyster Harbour,

W.A. Our thanks go to George Kendrick (Western Australia Museum), Winston Ponder and Ian Loch (The Australian Museum, Sydney) for useful literature and comments. We are also grateful to Elizabeth Turner (Tasmanian Museum and Art Gallery) and Ben McHenry and Neville Sledge (South Australian Museum) for information on the Museum records. This research would not have been successful without the expert guidance of Patricia Dixon (Centre for Marine Science, University of New South Wales) on the ecological genetics of *A. trapezia*. Her help is gratefully acknowledged.

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Manuscript received 30 January 1996; accepted 25 July 1996.

Description of the eggs and yolk-sac larvae of Whitebait *Hyperlophus vittatus* (Teleostei: Clupeidae)

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Abstract – The eggs and early larval (yolk-sac) stages of *Hyperlophus vittatus* are described. The eggs are spherical, range from 0.83 – 0.95 mm in diameter (mode = 0.93 mm), have a perivitelline space which occupies 8.6 – 30.9% (mode = 14.5%) of the diameter, a coarsely and completely segmented yolk and one oil globule (0.025 – 0.075 mm in diameter, mode = 0.048 mm). The eggs hatch in 2 – 3 days at a mean temperature of 17°C. The yolk-sac larvae are approximately 2.6 mm BL at hatching and lack pigmented eyes or a functional mouth. The larvae are elongate and have a long, straight gut (pre-anal length = 70 – 79% of BL) with the single oil globule located posteriorly in the yolk-sac. The presence of melanophores immediately dorsal of the posterior tip of the notochord distinguish the yolk-sac larvae of *H. vittatus* from those of other clupeids in southern Western Australia.

INTRODUCTION

Whitebait (*Hyperlophus vittatus* Castelnau), or sandy sprat, their common name elsewhere in Australia, is commercially fished in the southwest of Western Australia (Goh 1992). The confinement of whitebait fishing in this region to beach seining operations has restricted the amount of information available on the distribution of this species. Collecting eggs and larvae using plankton nets provides a much more economical means of sampling relatively large areas than sampling adults. Ichthyoplankton surveys can thus overcome the problem of limited data on the distribution of a teleost species but requires accurate identification of its early life stages. While *H. vittatus* larvae 5.3 – 29.1 mm SL have been described (Miskiewicz 1987), eggs and larvae <5.3 mm SL are undescribed.

The aim of this paper is to provide a description of the developmental stages of the fertilized eggs and yolk-sac larvae of *H. vittatus* to facilitate the use of ichthyoplankton surveys for determining the spatial distribution of spawning whitebait populations. The embryogeny of *H. vittatus* eggs is only described sufficiently to identify the eggs of this species in plankton collections.

MATERIALS AND METHODS

Commercial catches of whitebait in Western Australia were monitored through 1993. In early August 1993, 12% of a catch of 200–300 kg of whitebait from Warnbro Sound (32°20.8'S,

115°44.5'E) had ripe gonads, suggesting that spawning was probably occurring at this region. On 17 August 1993, plankton tows were completed at several sites within Warnbro Sound, using 60 cm diameter bongo nets with 500 µm mesh, towed just below the surface at 1 m s⁻¹. Fish eggs were particularly abundant at one station close to shore, sampled at 1200 hours. The surface water temperature at this site was 18°C, with a salinity of 35.1. The plankton sample from this tow was taken back to the laboratory, so that fish eggs could be removed and reared.

Culturing of the eggs past hatching was necessary since their identification required identification of the resultant larvae. Although *H. vittatus* larvae <5.3 mm SL have not been described, individuals smaller than this have previously been identified (e.g., Gaughan *et al.* 1990) using Miskiewicz (1987) as a baseline from which to examine a series of sequentially smaller whitebait larvae, which were identified by their elongate shape, the relative length of the gut and the pattern of pigmentation.

At the laboratory, fish eggs were siphoned off from the plankton sample and sorted using a stereomicroscope. Two types of eggs were abundant in the sample. Approximately 100 eggs of one of these types, which exhibited the characteristics of clupeid eggs, were selected for culturing. These characteristics were the spherical shape, the presence of a segmented yolk and a single oil globule (Ahlstrom and Moser 1980; McGowan and Berry 1984).

The selected eggs were placed in four glass containers of seawater, two lightly aerated and two non-aerated, and maintained at ambient temperature (15.2–24.0°C, mean = 17°C). The eggs survived well under these conditions and nearly all them hatched. Forty larvae obtained from these hatched eggs were transferred to a constant temperature tank (18°C). Algae and enriched rotifers were added to the water as a potential food source for the developing larvae.

Samples of eggs and larvae were taken daily and preserved in 5% formalin. The first few reared larvae were identified as being those of *H. vittatus*, thereby confirming that the eggs chosen for culturing were of this species. *Hyperlophus vittatus* eggs were thus also able to be identified. Whilst the sample of eggs collected for rearing did not contain any early embryonic stages, these were described using material collected from previous plankton tows in Warnbro Sound. These earlier stages of whitebait eggs were identified by their size, the presence of a segmented yolk and the relative size of the yolk, as determined from the reared eggs of known identity.

Measurements of eggs and larvae were made using an eyepiece micrometer fitted in a compound microscope. The measured lengths of the larvae refers to body length (BL, tip of snout to tip of the notochord; Leis and Trnski 1989). Descriptions of pigment refers to black pigment (melanin) unless stated otherwise. Because future identification of eggs and early larvae will most likely involve formalin-preserved samples, the illustrations and measurements were done with formalin-preserved material. The illustrations were made with the aid of camera lucida.

RESULTS

Development time of eggs

Most (> 95%) of the reared *H. vittatus* eggs hatched within 48 hours of capture. The seven, least developed eggs had embryonic keels (see Figure 1d) at the time the live sample was sorted (1400 hours, 2 hours after capture). Five of these eggs were allowed to develop through to hatching, which occurred 50–51 hours post-capture.

General description of eggs

Hyperlophus vittatus eggs are planktonic and spherical. The eggs have a thin chorion that appears smooth under low magnification. Under high magnification, however, evenly spaced corrugations can be seen. The diameter of formalin-preserved eggs ranges from 0.83 to 0.95 mm, with a mode of 0.93 mm.

Each egg contains one oil globule ranging in diameter from 0.025 to 0.075 mm, with a mode of

0.048 mm. The oil globule is not pigmented.

The yolk is spherical to ovoid, depending on the angle of view (Figure 1a,aa), with a diameter ranging from 0.50 to 0.87 mm (mode = 0.83 mm). In live eggs, the yolk appeared nearly transparent, but became opaque when preserved in formalin and is semi-translucent both under bright transmitted and reflected light. The yolk is coarsely and completely segmented with a 'frothy' or 'bubbly' appearance which is readily apparent during all stages of development.

The perivitelline space occupies 8.6–30.9% of the eggs diameter (mode = 14.5%).

Description of various stages during development of the eggs

Initially, the segmented yolk is the most prominent feature of the egg (Figure 1a,aa). Cell growth becomes obvious at the pole opposite to that containing the oil globule, i.e. the vegetative pole (Figure 1 b). This cap of cells appears to bulge slightly over the yolk. The cell-cap flattens out as cells multiply and spread in a thinner layer over the yolk towards the opposite pole (Figure 1c). In contrast to the opacity of the relatively thick cell-cap, the yolk is visible beneath this thin layer of cells.

The anterior end of the embryo becomes visible at the vegetative pole as a slightly raised strip (i.e., embryonic keel), with a flatter layer of cells lying at either side (Figure 1d). The embryo is less distinct towards the posterior end and the thin layer of cells, although difficult to observe, is much wider than at the anterior end.

The embryo then becomes more distinct, with the eye and some somites visible (Figure 1e). The tip of the tail lies beyond the oil globule. Divisions of the brain are visible from dorsal view of the head, which lies flat against the yolk. In the majority of the eggs, at this and later stages, the yolk-sac lying beneath the head is concave, but with a central bulge (Figure 1f). However, the yolk remained rounded in a few of the eggs examined (cf. Figures 1f,ff). The concavity may be due to absorption of the yolk by the developing embryo.

With further development, the tail lifts away from the yolk, develops finfolds at the tip and begins to curve to the right. The tail also becomes more pointed and increases in length, while the finfold extends anteriorly almost to the head (Figure 1f). The anterior end of the embryo begins to lift away from the yolk. The gut which is present along the ventral surface of the embryo is difficult to distinguish and has therefore not been shown in Figure 1f.

As development continues, the tail lengthens, the finfold widens and the hindgut becomes more obvious (Figure 1g). At the time of hatching, the dorsoventrally flattened head of the embryo still

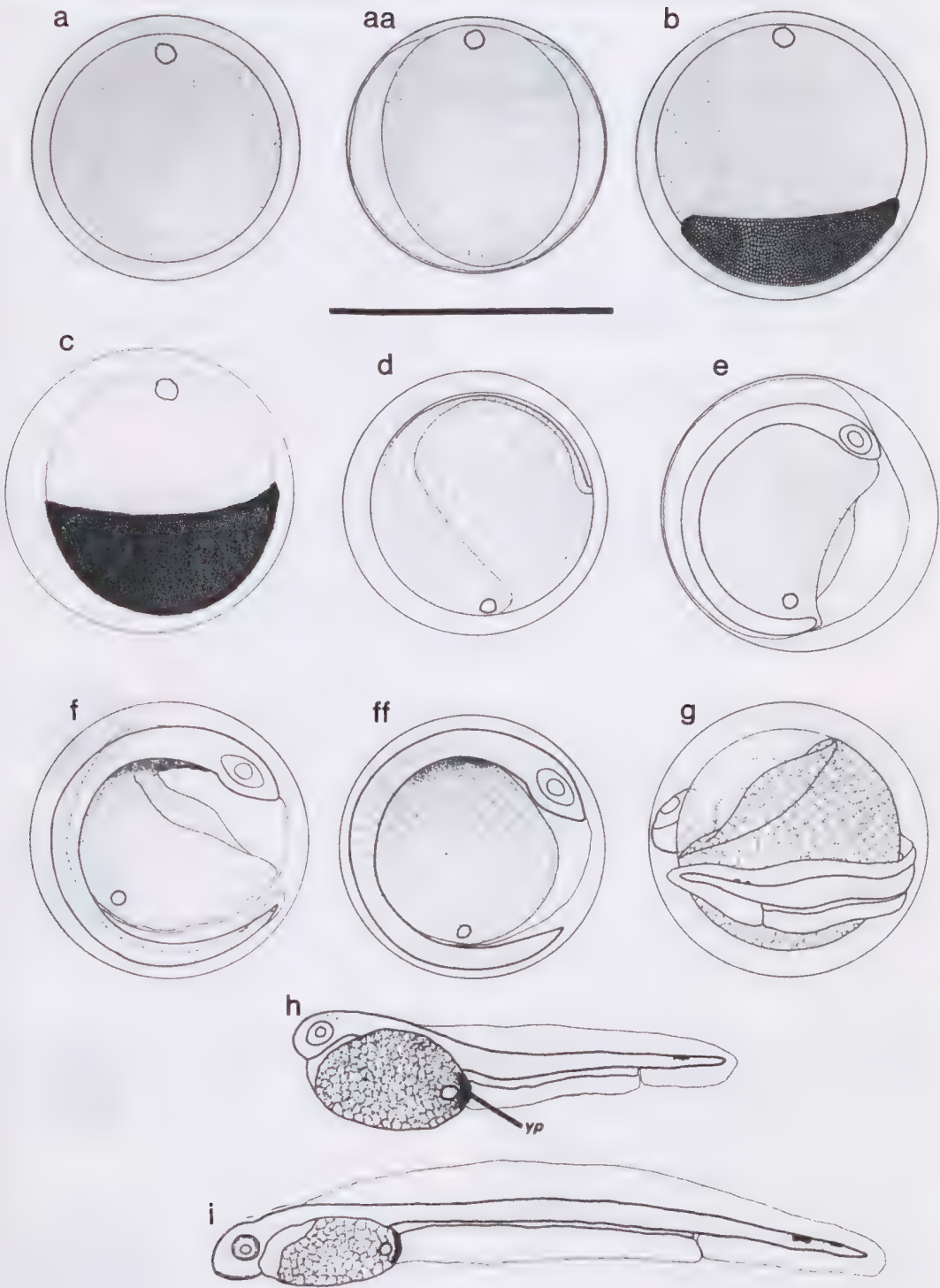


Figure 1 Early life history stages of *Hyperlophus vittatus*. a–g, eggs. h, newly hatched yolk-sac larva, 2.7 mm BL, yp – patch of yellow pigment; i, yolk-sac larvae, 4.2 mm BL. Scale bar equals 1.0 mm.

lies close to the yolk (or yolk-sac membrane), the tail has grown completely around the yolk and overlaps the head, but the mouth has not developed and the eyes are not yet pigmented. The 2 – 3 small melanophores on the dorsal surface of the tail near the tip of the notochord are characteristic of *H. vittatus* larvae, and whilst illustrated here (Figure 1g), they were often not visible in preserved eggs.

Description of yolk-sac larvae


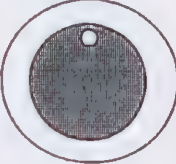
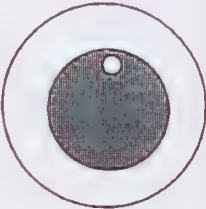
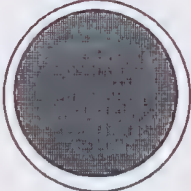
Newly-hatched larvae were 2.6 mm BL and had typical clupeid characteristics, including a long slender body, a long straight gut and light pigmentation (Figure 1h). The pre-anal length is 70 – 79% BL.

The oil globule is located near the posterior end of the yolk-sac. A patch of yellow pigment, which

is often only obvious in fresh or recently preserved specimens, was observed immediately posterior to the oil globule (Figure 1h,i). Newly hatched *H. vittatus* larvae have very fine melanophores scattered over the body, particularly over the head. However, these melanophores are difficult to observe after preservation, so only the denser concentrations on the head have been illustrated. Moreover, they have 2 – 3 distinct melanophores on the dorsal side of the trunk near the notochord tip which are homologous to those observed in well developed embryos within late-stage eggs (cf. Figure 1g).

At the time of hatching, larvae had neither pigmented eyes nor a mouth (Figure 1h). Larvae placed in the constant temperature tank (18°C) had utilised their yolk, developed pigmented eyes and appeared to have a functional mouth after 5 – 7

Table 1 The major distinguishing features of the pelagic eggs of clupeids which are common in marine waters of southern Western Australia. The eggs of each species have segmented yolks. The measures of egg and yolk diameter for *S. sagax* from New Zealand (Baker 1972), and egg diameter for *E. teres* from South Africa (O'Toole and King 1974) are presented below those recorded in the present study.

Species	Egg diameter (mm) range (mode)	Oil globule	Yolk diameter (mm) range (mode)	Perivitelline space (% of diameter) range (mode)	Diagrammatic representations
<i>Hyperlophus vittatus</i> n = 73	0.83–0.95 (0.93)	yes	0.50–0.87 (0.83)	8.6 – 30.9 (14.5)	
<i>Sardinella lemuru</i> n = 40	1.15–1.32 (1.30)	yes	0.69–0.82 (0.75)	34.2 – 44.8 (39.7)	
<i>Sardinops sagax</i> n = 30	1.34–1.58 (1.44) 1.32–1.70 (1.53) (Baker 1972)	yes	0.62–0.85 (0.69) 0.71–0.83	42.2 – 57.9 (49.4)	
<i>Etrumeus teres</i> n = 52	1.24–1.48 (1.35) 1.32–1.47 (1.37) (O'Toole and King 1974)	no	0.99–1.28 (1.12)	7.1 – 22.6 (18.7)	

days. They ranged in size from 4.2 to 4.7 mm BL. Rearing of *H. vittatus* larvae beyond the yolk-sac stage was unsuccessful with the larvae failing to feed on the supplied rotifers and algae. Consequently no larvae survived past 8 days.

DISCUSSION

Eggs

Hyperlophus vittatus eggs which were collected at 1200 hours and already possessed an embryonic keel, required a further 50 – 51 hours to hatch. Since many clupeoid species spawn at night (e.g., Blaxter and Hunter 1982; Sommerton *et al.* 1993), we assumed that the least developed *H. vittatus* eggs collected for culturing had been fertilized between 2000 and 0400 hours the night before capture. Thus, the development time to hatching for *H. vittatus* eggs, at a mean temperature of 17°C, was 58 – 67 hours (2.5 – 3 d).

Hyperlophus vittatus have eggs which are typical of many marine teleosts (Ahlstrom and Moser 1980; Matarese and Sandknop 1984), being spherical with a diameter of about 0.9 mm and possessing a single oil globule. Nonetheless, *H. vittatus* eggs can be distinguished from those of other species found in plankton collections in southwestern Australia by their size, the segmented yolk, the relative sizes of the yolk and the perivitelline space, and the small oil globule. However, in other regions, the initial identification of *H. vittatus* eggs should ideally be carried out on the late-stage eggs in which the embryo is well developed. In particular, the 2 – 3 melanophores dorsal of the notochord tip provide a means of identifying late-stage *H. vittatus* eggs.

The other clupeid species common in southern Western Australian waters are *Spratelloides robustus*, *Sardinella lemuru*, *Sardinops sagax* and *Etrumeus teres* (Hutchins and Swainston 1986). The eggs of *S. robustus* have a gelatinous covering and are laid demersally (McGowan and Berry 1984) so would not be expected to occur in plankton samples. The major features which distinguish *H. vittatus* eggs from those of these other clupeids are the size of the egg and the relative width of the perivitelline space (Table 1). As is the case with all clupeids (McGowan and Berry 1984), the eggs of each of these species have segmented yolks. The dimensions of the eggs of these other species were based on specimens found in plankton samples taken in marine waters off southwestern Australia and preserved in the same way as the *H. vittatus* eggs used in this study. Baker (1972) provides a full description of *S. sagax* eggs, while figures of the eggs of several *Sardinella* species can be found in Bensam (1990). Development of *E. teres* eggs has been described by O'Toole and King (1974).

Hyperlophus vittatus eggs (diameter of 0.93 mm) are smaller than those of *S. lemuru*¹ (1.30 mm), *S. sagax* (1.44 mm) and *E. teres* (1.35 mm) (Table 1). The perivitelline space occupies 14.5% of the egg diameter in *H. vittatus*, but accounts for 39.7 and 49.4% of the diameter in *S. lemuru* and *S. sagax* respectively. Although the relative size of the perivitelline space in the eggs of *E. teres* (18.7%) is more similar than these other species to that for *H. vittatus*, the eggs of this former species lack an oil globule (Table 1).

In addition to these features, late-stage *H. vittatus* eggs can be identified by the dorsal melanophores on the tail of the embryo and, in fresh specimens, the yellow pigment posterior to the oil globule.

Larvae

The most easily recognisable feature of the yolk-sac larvae of *H. vittatus*, which can be used to distinguish this species from the other clupeid larvae which occur in southern Western Australia, is the presence of dorsal melanophores near the notochord tip. Yolk-sac larvae of *S. robustus*, *S. lemuru*, *S. sagax* and *E. teres* lack these melanophores. Likewise, the yolk-sac larvae of *Engraulis australis*, which are similar in body form to those of *H. vittatus*, do not possess melanophores dorsal to the notochord tip.

ACKNOWLEDGEMENTS

Thanks to Ken White for assisting in the collection of the plankton material. This manuscript benefited from comments made by staff of the WA Marine Research Laboratory and by two anonymous referees.

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Manuscript received 13 September 1995; accepted 25 July 1996.

Species composition and checklist of the demersal ichthyofauna of the continental slope off Western Australia (20–35°S)

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Abstract – The first regional collection of fishes from the continental slope off the west coast of Australia was taken between 1989 and 1991 during exploratory trawling. Collections were taken from 95 trawls completed during an exploratory fishing survey by a research vessel at latitudinally and depth-stratified stations, and from 56 trawls aboard commercial vessels. The region trawled was between latitudes 20–35°S in depths from 200 to about 1500 m.

The demersal slope fish fauna in this region is highly speciose: 388 species from 108 families were identified and these are presented in a checklist. Approximately 100 of these species are recorded from Australian waters for the first time and many represent undescribed taxa. We present criteria which establish the reliability of identifications in the checklist. Overall, the Macrouridae are the most speciose family with 50 species; 10 or more species were also recorded from the Squalidae (22 species), Alepocephalidae (17), Ophidiidae (17), Moridae (13), Triglididae (13), Scyliorhinidae (10) and Scorpaenidae (10).

The most abundant families (in numbers of individuals) in 200–600 m include the Acropomatidae, Trachichthyidae, Chlorophthalmidae and Scorpaenidae. Between 600 and 800 m, the Macrouridae, Bathylupeiidae, Chaunacidae and Neoscopelidae are most abundant, while the Macrouridae, Alepocephalidae, Oreosomatidae and Synphobranchidae dominate depths below 800 m.

INTRODUCTION

In their recent treatment of the Australian fish fauna, Paxton *et al.* (1989) described the offshore waters of Western Australia as virtually unsampled from an ichthyological perspective. Fish collections had been made during an exploratory fishing survey by a Japanese trawler on the continental shelf and upper-continental slope to a depth of 600 m (Heald and Walker 1982). However, few specimens from that work are represented in museum collections and consequently species identifications cannot be verified. Similarly, few results from surveys undertaken by the Soviets in Western Australian waters between 1962 and 1974, (E. Nosov, TINRO, Vladivostok, Russia, pers. comm.) are available. Locality and depth of capture data in occasional descriptions of new species, e.g., Sazonov and Shcherbachev (1982) and Iwamoto and Shcherbachev (1991), indicated those cruises had fished on the western slope region. More recently, fish collections have been taken during exploratory fishing by Australian trawlers and foreign vessels in collaborative fishing ventures. These operations included a survey by the CSIRO Division of

Fisheries' research vessel, FRV *Southern Surveyor*, based around a series of stations stratified by depth and latitude. This paper is based on collections of demersal fishes taken during these operations between 1989 and 1991.

Collections of deep water fishes from the Australian region have expanded rapidly in recent years following the commercial exploitation of continental slope resources. Commercial fishing has occurred primarily on the slope region of southeastern Australia and the Great Australian Bight (GAB) where blue grenadier (*Macruronus novaezelandiae*), gemfish (*Rexia solandri*) and orange roughy (*Hoplostethus atlanticus*) were targeted. The demersal fish faunas of these regions were documented in preliminary checklists: the mid-slope (~700–1200 m) region off southeastern Australia by Last and Harris (1981) and Koslow *et al.*, (1994); the GAB by Newton and Klaer (1991), and the upper continental slope (~500 m) off southeastern Australia by May and Blaber (1989). Many of the 448 new Australian records in Paxton *et al.* (1989) were deep water species.

In this paper we provide an overview of the faunal composition of fishes from the upper and

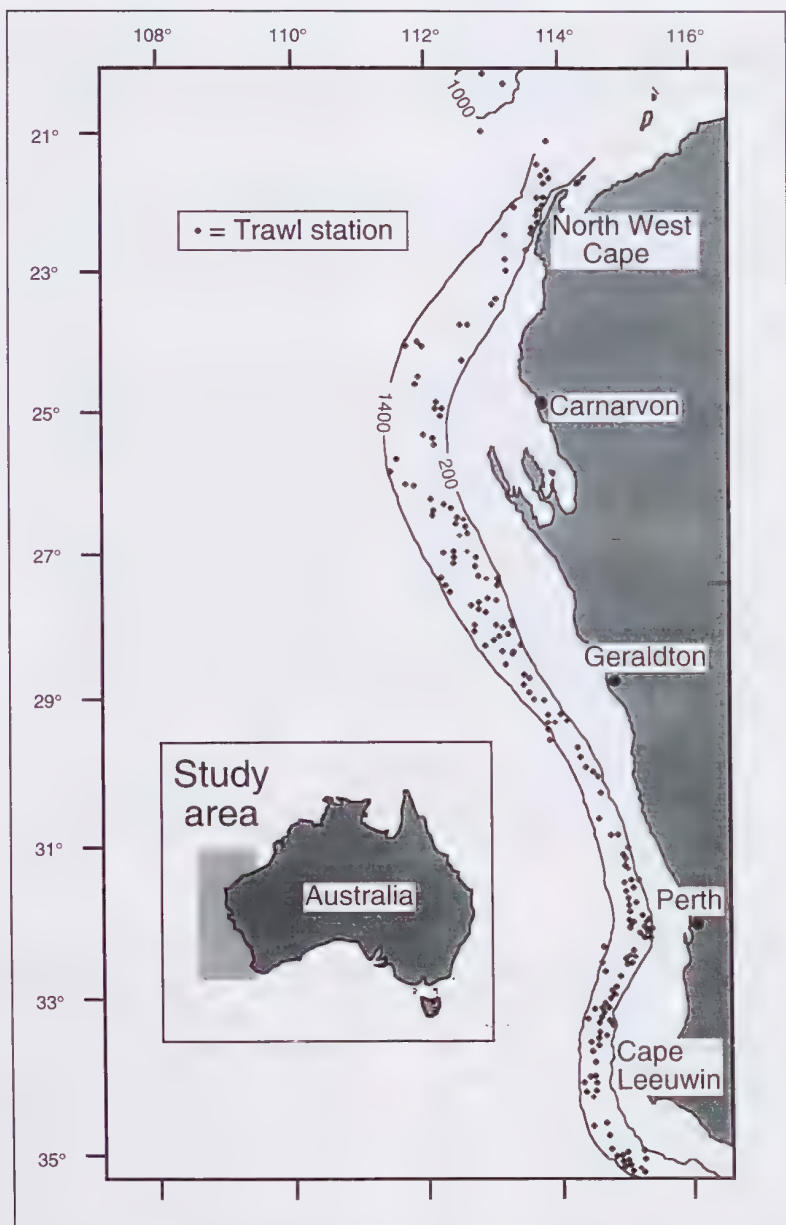


Figure 1 Map of the study area showing the approximate positions of the 200 m and 1400 m isobaths and the trawl stations from which fish collections were taken.

mid-slope region off the western coast of Australia, along with a checklist of species taken. Distributional range information and museum registration details are provided. The data are based primarily on a 30-day research survey undertaken in 1991, supplemented with collections from commercial fishing vessels. Samples were taken from an area between latitudes 20° and 35°S over a depth range of approximately 200–1500 m.

MATERIALS AND METHODS

Data collection and analysis

Fishes were collected from 95 demersal trawl stations during an exploratory survey (CSIRO Division of Fisheries, FRV *Southern Surveyor* research cruise SS01/91) and from 56 commercial trawls. Details of trawl stations are given in Table 1 and their approximate positions shown in a

Table 1 Position and depths of stations sampled with demersal trawls during this study. Vessel code refers to the CSIRO research vessel (RV) or commercial fishing vessels (CV).

Vessel	Latitude (°S)	Longitude (°E)	Depth (m) (start)	Depth (m) (end)	Vessel	Latitude (°S)	Longitude (°E)	Depth (m) (start)	Depth (m) (end)
RV	20°16'	113°13'	913	914	RV	32°04'	115°09'	270	285
RV	20°07'	112°55'	868	854	RV	32°02'	115°08'	510	510
RV	20°55'	112°51'	1139	1128	RV	32°02'	114°52'	700	1200
RV	21°28'	113°38'	1022	1023	RV	32°14'	115°06'	286	287
RV	21°37'	113°55'	328	328	RV	32°10'	115°08'	225	230
RV	21°39'	113°58'	209	215	RV	32°19'	114°28'	1280	1310
RV	21°44'	113°52'	320	290	RV	32°34'	114°27'	1030	1140
RV	21°44'	113°52'	274	273	RV	32°40'	114°28'	880	960
RV	21°50'	113°46'	685	650	RV	33°17'	114°12'	982	982
RV	21°54'	113°40'	1158	1100	RV	33°18'	114°31'	220	220
RV	22°00'	113°08'	1460	~1500	RV	33°17'	114°30'	468	430
RV	22°28'	113°12'	1258	1305	RV	33°24'	114°31'	203	204
RV	22°47'	113°13'	880	910	RV	33°22'	114°29'	399	350
RV	22°59'	113°14'	482	544	RV	33°25'	114°21'	817	780
RV	23°25'	113°03'	297	311	RV	33°49'	114°17'	1050	1050
RV	23°25'	113°03'	300	302	RV	34°12'	114°07'	1240	1225
RV	23°46'	112°36'	576	587	RV	34°39'	114°15'	890	890
RV	23°44'	112°35'	612	620	RV	34°56'	114°29'	900	958
RV	23°44'	112°35'	612	623	RV	34°59'	114°43'	738	750
RV	23°00'	111°54'	1060	1064	RV	35°04'	114°59'	870	920
RV	23°59'	111°54'	1061	1071	CV	35°08'	115°01'	1003	—
RV	24°09'	111°39'	1293	1320	CV	35°07'	115°01'	945	—
RV	24°30'	111°50'	892	905	CV	35°02'	115°02'	673	—
RV	24°30'	111°50'	895	901	CV	34°59'	114°53'	712	—
RV	24°51'	112°07'	467	478	CV	34°45'	114°26'	727	—
RV	24°52'	112°07'	444	468	CV	34°15'	114°20'	825	—
RV	24°55'	112°11'	318	344	CV	34°10'	114°16'	1030	—
RV	25°07'	112°09'	306	319	CV	33°58'	114°22'	870	—
RV	25°07'	112°09'	312	312	CV	33°44'	114°22'	740	—
RV	25°19'	111°56'	612	610	CV	33°17'	114°13'	976	—
RV	25°41'	111°30'	1115	1125	CV	33°20'	114°30'	435	—
RV	25°52'	111°27'	1254	1277	CV	33°13'	114°31'	440	—
RV	26°02'	111°39'	1000	1005	CV	33°06'	114°30'	596	—
RV	26°05'	111°46'	882	874	CV	32°52'	114°35'	571	—
RV	26°14'	112°03'	690	691	CV	30°57'	114°48'	470	—
RV	26°35'	112°29'	508	500	CV	29°50'	114°21'	413	—
RV	26°40'	112°32'	478	456	CV	29°43'	114°18'	450	—
RV	26°42'	112°41'	200	194	CV	28°48'	113°37'	457	—
RV	26°42'	112°38'	285	285	CV	28°06'	113°27'	649	—
RV	26°45'	112°36'	346	367	CV	28°13'	113°07'	616	—
RV	26°57'	112°22'	666	688	CV	27°49'	113°01'	437	—
RV	27°06'	112°22'	714	713	CV	26°59'	112°38'	435	—
RV	27°22'	112°10'	1009	996	CV	26°36'	112°09'	760	—
RV	27°28'	112°13'	750	900	CV	25°36'	112°10'	435	—
RV	27°32'	112°15'	1107	1140	CV	26°25'	112°20'	565	—
RV	27°32'	112°15'	1104	1110	CV	32°06'	115°10'	244	—
RV	28°00'	112°41'	945	946	CV	31°59'	115°12'	230	—
RV	28°04'	112°42'	854	853	CV	32°29'	114°53'	385	—
RV	28°16'	113°17'	520	520	CV	32°21'	114°59'	362	—
RV	27°17'	112°45'	510	520	CV	32°20'	114°59'	360	—
RV	27°08'	112°44'	438	370	CV	32°21'	114°59'	348	—
RV	27°04'	112°44'	303	333	CV	20°40'	113°43'	225	—
RV	27°23'	112°51'	306	279	CV	22°30'	113°35'	250	—
RV	27°38'	113°00'	248	252	CV	22°22'	113°40'	225	—
RV	29°15'	113°56'	320	325	CV	21°35'	113°40'	240	—
RV	29°20'	113°58'	490	505	CV	22°13'	113°44'	270	—
RV	29°21'	113°46'	942	970	CV	31°34'	115°00'	213	—
RV	29°22'	113°42'	1160	1167	CV	31°12'	114°56'	213	—
RV	29°28'	113°42'	1160	1160	CV	32°38'	114°47'	376	—
RV	29°35'	113°44'	1132	1136	CV	32°55'	114°39'	373	—
RV	29°51'	114°11'	770	760	CV	32°41'	114°47'	342	—
RV	30°01'	114°29'	255	265	CV	32°18'	114°58'	350	—
RV	30°00'	114°27'	380	380	CV	35°05'	114°53'	989	—
RV	30°00'	114°27'	480	490	CV	35°03'	114°51'	900	—
RV	30°16'	114°30'	684	684	CV	29°14'	113°52'	556	—
RV	30°39'	114°27'	1058	1080	CV	27°53'	113°08'	225	—
RV	30°51'	114°37'	893	887	CV	31°31'	114°53'	470	—
RV	31°16'	114°50'	613	614	CV	28°03'	113°15'	204	—
RV	31°17'	114°52'	475	512	CV	27°33'	112°58'	218	—
RV	31°44'	114°59'	390	485	CV	27°29'	112°50'	250	—
RV	32°02'	114°54'	670	640	CV	34°57'	114°56'	201	—
RV	31°53'	115°05'	411	550	CV	28°30'	112°55'	960	—
RV	31°55'	115°10'	320	850	CV	31°20'	114°54'	390	—
RV	32°09'	115°02'	484	470	CV	31°49'	115°01'	390	—
RV	32°07'	115°06'	308	295	CV	31°31'	114°57'	390	—
					CV	31°29'	114°55'	390	—

diagram (Figure 1). In brief, sampling was carried out within the Western Deep Water Trawl Fishery (WDWTF), a management zone bounded in the north at 20°S by the 114°E meridian (North West Cape) and in the south at ~35°S by the 115°08'E meridian (Cape Leeuwin). Trawling operations involved the use of a variety of nets, although typically these nets had a large headline length (> 35.5 m) and heavy rubber-bobbin ground gear. Details of the net and trawl configuration used in the research survey are provided elsewhere (Williams *et al.*, submitted). A random-stratified sampling design was used for the survey based on six depth strata of 200 m within eight latitudinal strata of 100 nautical miles each. In addition, one trawl (#12) sampled in a depth range of 1460–1500+ m. Sixty five of the 95 stations were random-stratified; the remainder were targeted on fish schools detected by echosounder. About 90,000 fishes were caught during the research vessel survey, with the number of fish taken in the commercial catches unknown. About 90% of the fish species were recorded from survey operations.

Aboard the research vessel, fish specimens retained for museum collections were sorted on ice and placed in 10% formalin solution at the earliest opportunity. On commercial vessels specimens were frozen and preserved later in the laboratory. Most of the material retained is deposited in the I.S.R. Munro Ichthyological Collection at the CSIRO Division of Fisheries Laboratories in Hobart (CSIRO), at the Australian Museum in Sydney (AMS), and the Museum of Victoria, Melbourne (NMV). A few voucher specimens are also lodged at the Western Australian Museum, Perth (WAM).

Numerical abundances were calculated from numbers and weights, and standardised by the area swept and duration of trawls. Abundance data relate only to the 65 random stratified stations from the research vessel survey.

As the purpose of this paper is to present information on demersal fishes, pelagic species from the following taxa were excluded from the checklist: Serrivomeridae, Nemichthyidae, Eurypharyngidae, Bathylagidae, Opisthoproctidae, Gonostomatidae, Sternoptychidae, Astronesthidae, Melanostomiidae, Malacosteidae, Chauliodontidae, Stomiidae, Idiacanthidae, Myctophidae, Notosudidae, Paralepididae, Omosudidae, Alepisauridae, Evermannellidae, Scopelarchidae, Rondeletiidae, Ogcocephalidae (only *Coelophrys* sp.), Ceratoidea, Macrouridae (only *Hymenocephalus* species, *Mesobius* species, *Squalogadus modificus*), Melamphaidae, Anoplogastridae, Carangidae, Bramidae, Chiasmodontidae, Gempylidae (only *Lepidocybium flavobrunneum*, *Ruvettus pretiosus*, *Thyrstitoides marleyi*) and Trichiuridae.

Taxonomic identifications

As noted by Paxton *et al.* (1989), the taxonomic understanding of Australian fishes has only just begun for some groups. This is especially true for those occurring in the continental slope region. Many of the species encountered in this study are poorly known; indeed many are recorded from Australian waters here for the first time and many of these are yet to be described. A continuity in field identifications was ensured by the preparation of identification sheets for each taxon and by updating them on a station by station basis. Our family classification follows Nelson (1994).

The order of reliability of identification of each species was provided using a five level system presently in use at the CSIRO fish collection. It takes into consideration the taxonomic experience of the identifier, their knowledge of the group considered, and the amount of effort given to making the identification. In this scheme identifications below level 2 are not considered fully reliable; an explanation is given in Table 2.

Table 2 Criteria for assessing the reliability of identifications based on the taxonomic expertise of the identifier and their intentions as used in the checklist.

Level 1: Highly reliable identification – Specimen identified by (a) an internationally recognised authority of the group, or (b) a specialist that is presently studying or has reviewed the group in the Australian region.

Level 2: Identification made with high degree of confidence at all levels – Specimen identified by a trained identifier who had prior knowledge of the group in the Australian region or used available literature to identify the specimen.

Level 3: Identification made with high confidence to genus but less so to species – Specimen identified by (a) a trained identifier who was confident of its generic placement but did not substantiate their species identification using the literature, or (b) a trained identifier who used the literature but still could not make a positive identification to species, or (c) an untrained identifier who used most of the available literature to make the identification.

Level 4: Identification made with limited confidence – Specimen identified by (a) a trained identifier who was confident of its family placement but unsure of generic or species identifications (no literature used apart from illustrations), or (b) an untrained identifier who had/used limited literature to make the identification.

Level 5: Identification superficial – Specimen identified by (a) a trained identifier who is uncertain of the family placement of the species (cataloguing identification only), (b) an untrained identifier using, at best, figures in a guide, or (c) where the status and expertise of the identifier is unknown.

RESULTS

Faunal overview

A total of 388 fish species from 108 families are recorded from the western continental slope region between the 200 and 1500 m isobaths (Appendix 1). A high number, around 100 species, are recorded from Australian waters for the first time, and many are undescribed.

The most species-rich family is the Macrouridae with 50 species; in our collections it has about 2.5 times the number of species of any other family and accounts for about one seventh of all species caught. Other speciose families, in decreasing order of numbers of species taken, are the Squalidae (22 species), Alepocephalidae (17), Ophidiidae (17), Moridae (13), Triglidae (13), Scyliorhinidae (10) and Scorpaenidae (10). Of the remaining families, 44, or over 40% of the total, are represented by only a single species. The composition of dominant families changes markedly in the shallower strata (200–600 m) but is dominated in depths exceeding 800 m primarily by macrourids, alepocephalids and oreosomatids (Table 3).

Dominant taxa within depth strata

Within the shallow upper-slope depth range (200–400 m) the numerically dominant families are the Acropomatidae, Trachichthyidae, and Macrurocyttidae (Table 3). Acropomatids are primarily *Malakichthys* sp. A, *Acropoma japonicum*, *Apogonops anomolus* and *Synagrops philippinensis* (~36%, 9%, 3% and 2% of total individuals, respectively). Trachichthyid representatives include *Gephyroberyx darwini* (23%) and a suite of small *Hoplostethus* species dominated by *H. latus*

(less than 1%). The Macrurocyttidae is represented by a single species, *Zenion* sp. A.

The Chlorophthalmidae is the dominant family in the 400–600 m stratum but represents only 20% of individuals. Of the five species collected, *Chlorophthalmus nigripinnis* and *Chlorophthalmus* sp. C are most numerous (13% and 6%, respectively) and, as with the other chlorophthalmid species, are restricted to the shallow and mid-depths of the upper-slope. The prevalence of the Acropomatidae in this depth range is due to *Apogonops anomolus* (13%) and *Malakichthys* sp. A (3%). The Scorpaenidae is among the most speciose families taken on the western slope region. It is represented by several species in this depth range with *Helicolenus barathri* accounting for about 7% of individuals. The most abundant macrourids in this depth range are *Caelorinchus* species, the most numerous being *C. maurofasciatus*, *C. mirus* and *C. parvifasciatus*.

Macrourids are numerically dominant in depths below 600 m. *Caelorinchus maurofasciatus* (11%), *Malacocephalus laevis* (8%), *Nezumia* sp. A (6%), *Ventrifossa macropogon* (6%) and *Lepidorhynchus denticulatus* (2%) have the highest numbers of individuals in 600–800 m. The species with the highest number of individuals is *Bathyclupea* sp. A (Bathyclupeidae), accounting for about 20% of the total catch. The Chaunacidae is represented mostly by *Chaunax* cf. *fimbriatus* (8%) and the Neoscopelidae by an unidentified species, *Neoscopelus* sp. A (4%).

In depths greater than 800 m the Macrouridae is the most speciose family, accounting for between 41% and 50% of the individuals in each of the three mid-slope strata. *Cetonus globiceps*, *Gadomus* sp.

Table 3 Numerically dominant four families in each 200 m depth stratum. Figures are the percentage of the total number of individuals per stratum (based on survey data only).

Depth stratum (m)	200–400	400–600	600–800	800–1000	1000–1200	1200–1400
Acropomatidae (temperate sea basses)	50	17				
Trachichthyidae (sawbellies)	24					
Macrurocyttidae (dwarf dories)	5					
Gempylidae (snake mackerels)	3					
Chlorophthalmidae (greeneyes)		20				
Scorpaenidae (scorpionfishes)		10				
Macrouridae (grenadiers)		8	42	41	50	49
Bathyclupeidae (bathyclupeids)			19			
Chaunacidae (coffinfishes)			8			
Neoscopelidae (new lanternfishes)			6	10		
Oreosomatidae (oreo dories)				10	12	
Alepocephalidae (slickheads)				14	12	7
Synphobranchidae (basketwork eels)					10	7
Ipnopidae (tripodfishes)						7
Mean number of fish per standard trawl	3229	510	223	202	157	160
Number of samples	12	12	10	15	11	5

B, three unidentified species of *Trachonurus* and *Bathygadus cottoides* have the greatest number of specimens; several species of the genera *Caelorinchus*, *Coryphaenoides*, *Nezumia* and *Ventrifossa* are also well represented. Several species account for the prominence of the Alepocephalidae. In 800–1000 m *Xenodermichthys copei* and *Rouleina guentheri* are the most abundant (10% and 3% respectively); in the two deepest strata *Alepocephalus triangularis*, *A. cf. productus* and *Narcetes lloydii* each make up between 1 and 4% of numbers. Oreosomatids are represented by four species, but *Allocyttus verrucosus* is the most abundant, making up 10% and 12% of numbers in the 800–1000 m and 1000–1200 m strata, respectively. The Synphobranchidae, comprising four species, ranks fourth and third in the two deepest strata (1000–1200 m and 1200–1400 m). *Diastobranchius capensis* and *Synphobranchius brevidorsalis* are most numerous with a combined proportion of about 7% of numbers in each stratum; *S. affinis* and *S. kaupi* contribute about 3% of the total number of individuals between 1000–1200 m. *Neoscopelus macrolepidotus* (Neoscopelidae) accounts for 10% of the total number of specimens taken in the 800–1000 m stratum and *Bathypterois ventralis* (Bathypteroidae) 7% of the numbers in the 1200–1400 m stratum.

Other groups are prominent in terms of species numbers or biomass but account for relatively few individuals. Overall, the Squalidae, with 22 species, ranks second in terms of numbers of species and, in the six strata sampled, ranks eleventh, sixth, ninth, seventh, eighth and eleventh, respectively, in numbers of individuals. *Squalus megalops* and *S. mitsukurii* are the dominant squalids on the upper-slope (1–3% and ~1% of numbers, respectively), with *Deania calcea* relatively common (~1%) on the shallow mid-slope, and *Zameus squamulosus* widespread and relatively common (~1%) in the 800–1500 m range. The Triglidae is represented by 13 species, dominated by members of *Lepidotrigla* and *Satyrichthys*. This family is restricted mainly to the shallow and mid-range of the upper-slope with only the distribution of *S. cf. investigatoris* extending below 500 m. Representatives of the Ophidiidae range from the upper-slope to the deep mid-slope. The upper-slope species, *Dannevigia tusca* and *Genypterus blacodes*, are relatively large but rare in this region, whereas several of the deep-dwelling species are more numerous and contribute to the prominent ranking of this family (fifth and seventh) in the two deepest strata. In these strata, the dominant species, *Monomitopus* sp. A, accounts for ~1–3% of total numbers of individuals.

Dominant taxa at different latitudes

The shallow upper-slope (~200–400 m) fauna

north of Shark Bay includes many tropical Indo-West Pacific species and species whose distributions include the outer shelf area of northwestern Australia (e.g., Sainsbury *et al.* 1985). The most abundant components in survey trawls include *Dentex tumifrons*, *Acropoma japonicum*, *Malakichthys* sp. A, *Synagrops philippinensis* and *Nemipterus bathybius*; commercial catches from this region are dominated by the lutjanid *Etelis carbunculus* with a by-catch of other tropical lutjanids, serranids and priacanthids. The shallow upper-slope fauna south of Perth comprises mainly temperate fishes whose distributions also encompass the outer shelf. Dominant elements include *Dannevigia tusca*, *Neosebastes thetidis*, *Pterygotrigla polyommata*, *Neoplatycephalus conatus*, *Lepidoperca filamenta*, *Zanclistius elevatus*, *Oplegnathus woodwardi*, *Nemadactylus macropterus*, and *Nelusetta ayraudi*.

A similar overlap of warm and cool water species is evident on the deeper reaches of the upper-slope (~400–800 m), but the most abundant species are generally more widely distributed. Abundant tropical/sub-tropical species include *Synagrops japonicus*, *Setarches guentheri*, *Epigonus macrops*, *Bathyclupea* sp. A and *Champsodon* cf. *longipinnis*. The dominant temperate elements of the deeper upper-slope fauna include some species which did not occur further north than the southernmost section of the west coast, and others which ranged northward well into warm waters. The former group includes several species endemic to southern Australia (e.g., *Galeus boardmani*, *Urolophus expansus* and *Lepidoperca filamenta*), and other species with restricted southern Australian and New Zealand distributions (*Chlorophthalmus nigripinnis*, *Caelorinchus maurofasciatus*, *Lepidorhynchus denticulatus* and *Helicolenus* cf. *percoides*). Temperate species with distributions extending into waters north of Shark Bay (~26°S) include *Hoplostethus latus*, *Pentaceros decacanthus*, *Zenopsis nebulosus* and *Notopogon xenosoma*. Other abundant species have temperate/subtropical distributions: *Caelorinchus mirus*, *Apogonops anomalous*, *Rexea solandri*, *Euclichthys polynemus*, *Tripteryphycis gilchristi* and *Malacocephalus laevis*.

Fishes from mid-slope depths (~800–1500 m) are typically wide ranging with southern circumglobal, Indo-Atlantic or cosmopolitan distributions. Some, however, exhibit restricted latitudinal ranges, primarily confined to the region between Cape Leeuwin and Shark Bay. Tropical mid-slope species that are both abundant and have restricted distributions include *Anacanthobatis* sp. A, *Bathypterois guentheri*, *B. ventralis*, *Lamprogrammus* cf. *niger* and *Mataeocephalus acipenserinus*. The abundant, wide-ranging species are *Pavoraja* sp. B, *Synphobranchius brevidorsalis*, *Aldrovandia affinis*, *A. phalacra*, *Alepocephalus triangularis*, *Xenodermichthys*

copei, *Monomitopus* sp. A and *Scombrabrax heterolepis*. Slope fishes that are abundant on the southern temperate Australian mid-slope and widely distributed on the west coast (extending north beyond Shark Bay) include *Centroscymnus owstoni*, *Deania calcea*, *Diastobranchius capensis*, *Synaphobranchius affinis*, *S. kaupi*, *Alepocephalus* cf. *productus*, *Rouleina guentheri*, *Neoscopelus macrolepidotus*, *Antimora rostrata*, *Bathygadus cottoides*, *Cetonurus globiceps*, *Coryphaenoides serrulatus*, *Neocyttus rhomboidalis* and *Alloctytus verrucosus*.

Many other species which are abundant on the temperate Australian mid-slope did not appear to occur north of Cape Leeuwin (~35°S). Conspicuous by their absence are the species which are commercially important in southeastern Australia. *Hoplostethus atlanticus* (orange roughy) and *Pseudocyttus maculatus* (smooth oreo) were even scarce in our more southern collections, whilst *Alloctytus niger* (black oreo) was not taken at all.

DISCUSSION

The high species richness is the most striking feature of the slope fish fauna in this region, and it is likely that further sampling with a variety of gears would substantially enlarge the number of species. Williams *et al.* (submitted) noted that sampling density during this study was low overall and that uncommon or aggregated species may have been missed. Furthermore, the selectivity of large-mesh trawls fitted with heavy ground gear most likely undersampled small species and groups which retain close contact with the bottom.

The great abundance of the Macrouridae (grenadiers) is also noteworthy. Despite their dominance, the group was poorly known in Australia at the time of the survey: only 32 of the 57 Australian species recorded by Paxton *et al.* (1989) were identified. It is apparent from our collections that at least 60 species are found on the Western Australian slope region (Iwamoto and Williams in prep.).

The west coast fish fauna is a mixture of warm and cold water species at all upper and mid-slope depths. However, latitudinal separation of tropical and sub-tropical species from temperate species is less evident as sampling depth increases. On the upper-slope (600–800 m) there is a change in the top-ranked families between 200 m depth strata, whereas on the mid-slope (800–1400 m) the Macrouridae, and to a lesser extent, Alepocephalidae, Oreosomatidae and Synaphobranchidae, are dominant throughout. In all strata, except for the 400–600 m stratum, the most abundant family accounts for 40–50% of individuals.

These ecological themes are developed in a

second paper. In that work, the patterns of diversity, biomass and assemblage structure of this slope fish fauna are discussed and compared to others from slope regions off southeastern Australia and the northern hemisphere (Williams *et al.* submitted).

ACKNOWLEDGEMENTS

The authors express their gratitude to the following experts who provided identifications for certain groups of fishes: Drs. Tomio Iwamoto (Macrouridae), Yuri Sazonov (Alepocephalidae, Platytrichtidae and Macrouridae), Barry Hutchins (Monacanthidae), Tony Harold (Bregmacerotidae) and Hisashi Imamura (*Bembras*). We thank the officers, crew and scientific staff of the FRV *Southern Surveyor* for their help during the trawl survey and numerous people from the fishing industry for the opportunity to sample from their fishing vessels. Dave Wright, Dave Evans, Dr Vicki Wadley, Dr Sebastian Rainer and Naomi Clear (CSIRO) assisted in making collections of fishes from commercial fishing vessels; Dave Wright, Alastair Graham and Gordon Yearsley (CSIRO), Mark McGrouther (AMS), Kevin Smith and Sue Morrison (WAM) helped to process and catalogue fish specimens; Gordon Yearsley, Karen Gowllett-Holmes, Dr Vivienne Mawson (CSIRO) and two anonymous referees critically reviewed an earlier version of the manuscript. This work was part of a project supported by the Fisheries Industries Research and Development Committee, Grant No.1988/74.

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Manuscript received 29 February 1996; accepted 25 July 1996.

Appendix 1 Checklist of demersal fishes collected from the western Australian continental slope in 200–1500 m between 20°S and 35°S. ID level refers to the reliability criteria detailed in Table 2; new record (*) refers to the first record of a species in Australian waters (Aust). Distributional limits of species based on our collections are shown by minimum and maximum depths, latitudes and longitudes; registration numbers identify museum voucher specimens in the CSIRO (H- codes), AMS (I- codes), WAM (P- codes) collections; '-' indicates no specimen was registered or retained; 'photo' indicates where non-retained specimens were photographed.

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude	Min. longitude	Max. latitude	Max. longitude	Registration number
HEXANCHIDAE									
<i>Heptanchius perlo</i> (Bonnaterre, 1788)	1		318	484	24°53'	112°08'	32°10'	115°03'	H2013-02
HETERODONTIDAE									
<i>Heterodontus zebra</i> (Gray, 1831)	1		221	229	22°22'	113°39'	22°22'	113°39'	P_30424-001
ALOPTIDAE									
<i>Alopias pelagicus</i> Nakamura, 1935	3		240	240	21°35'	113°40'	21°35'	113°40'	photo
PARASCYLLIDAE									
<i>Parascyllium</i> sp. A (of Last and Stevens, 1994)	1		245	245	32°08'	115°08'	32°08'	115°08'	H2360-01
SCYLORHINIDAE									
<i>Apristurus longicephalus</i> Nakaya, 1975	1		685	685	21°51'	113°47'	21°51'	113°47'	H2549-08
<i>Apristurus</i> sp. A (of Last and Stevens, 1994)	3		328	1060	21°38'	113°56'	34°57'	114°29'	H2592-02
<i>Apristurus</i> sp. B (of Last and Stevens, 1994)	3		942	942	29°22'	113°47'	29°22'	113°47'	H2624-01
<i>Apristurus</i> sp. D (of Last and Stevens, 1994)	1		1240	1240	34°13'	114°07'	34°13'	114°08'	H2623-03
<i>Apristurus</i> sp. F (of Last and Stevens, 1994)	2		1030	1050	32°35'	114°27'	33°50'	114°17'	H2615-01
<i>Apristurus</i> sp. G (of Last and Stevens, 1994)	1		684	942	26°15'	112°03'	30°17'	114°30'	H2573-01
<i>Asymbolus</i> sp. F (of Last and Stevens, 1994)	1		225	400	32°10'	115°08'	33°23'	114°30'	H2613-01
<i>Cephaloscyllium fasciatum</i> Chan, 1966	1		320	320	29°16'	113°57'	29°16'	113°57'	H2590-07
<i>Galeus boardmani</i> (Whitley, 1928)	1		213	510	24°53'	112°08'	33°23'	111°54'	H2591-10
<i>Galeus gracilis</i> Compagno and Stevens, 1993	1		467	467	24°51'	112°07'	24°51'	112°07'	–
TRIAKIDAE									
<i>Galeorhinus galeus</i> (Linnaeus, 1758)	1		213	213	31°34'	114°59'	31°34'	114°59'	–
<i>Iago garricki</i> (Fourmanoir and Rivaton, 1979)	2		467	467	24°51'	112°07'	24°51'	112°07'	H2564-09
<i>Mustelus antarcticus</i> Günther, 1870	1		225	225	32°10'	115°08'	32°10'	115°08'	H2613-15
<i>Mustelus</i> sp. B (of Last and Stevens, 1994)	3		297	346	23°25'	113°04'	27°23'	112°52'	H2356-02
CARCHARHINIDAE									
<i>Carcharias altimus</i> (Springer, 1950)	1		240	240	21°35'	113°40'	21°35'	113°40'	photo
<i>Galeorhinus cuvier</i> (Péron and Lesueur, 1822)	1		240	240	21°35'	113°40'	21°35'	113°40'	photo
SQUALIDAE									
<i>Centrophorus granulosus</i> (Bloch and Schneider, 1801)	1		868	868	20°08'	112°55'	20°08'	112°55'	H2543-05
<i>Centrophorus moluccensis</i> Bleeker, 1860	1		320	510	31°53'	115°06'	32°10'	115°03'	H2564-07
<i>Centrophorus squamosus</i> (Bonnaterre, 1788)	1		882	882	26°05'	111°47'	26°05'	111°47'	H2572-01
<i>Centrophorus uyato</i> (Rafinesque, 1810)	1		200	854	24°51'	112°07'	34°59'	114°44'	H2606-01

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude	Min. longitude	latitude	Max. longitude	Registration number
<i>Centrocyllium kamoharui</i> Abe, 1966	2		942	1254	23°60'	111°54'	33°18'	114°31'	H2560-02
<i>Centrocyminus crepidater</i> (Bocage and Capello, 1864)	1		870	880	32°40'	114°28'	35°05'	114°60'	H1815-02
<i>Centrocyminus ovestoni</i> Garman, 1906	1		868	1254	20°08'	112°55'	35°05'	114°60'	H2570-10
<i>Dalatias licha</i> (Bonnaterre, 1788)	1		373	508	26°36'	112°29'	32°55'	114°39'	—
<i>Deania calcea</i> (Lowe, 1839)	1		738	900	30°52'	114°37'	35°05'	114°60'	—
<i>Deania quadrispinosa</i> (McCulloch, 1915)	1		738	854	28°04'	112°43'	34°59'	114°44'	H2357-04
<i>Etmopterus brachyurus</i> Smith and Radcliffe, 1912	1		475	612	25°19'	111°56'	31°17'	114°53'	H2604-01
<i>Etmopterus lucifer</i> Jordan and Snyder, 1902	1		738	817	33°26'	114°21'	34°59'	114°44'	H2625-04
<i>Etmopterus pusillus</i> (Lowe, 1839)	3		320	882	26°05'	111°47'	33°26'	114°21'	H2621-04
<i>Etmopterus</i> sp. A (of Last and Stevens, 1994)	1		320	850	25°36'	112°10'	31°57'	115°09'	H2572-02
<i>Etmopterus</i> sp. B (of Last and Stevens, 1994)	1		870	880	32°40'	114°28'	35°05'	114°60'	H2616-10
<i>Euprotomicrus bispinatus</i> (Quoy and Gaimard, 1824)	1		913	913	20°16'	113°13'	20°16'	113°13'	H2541-01
<i>Squalus megalops</i> (Macleay, 1881)	1		203	510	24°53'	112°08'	33°24'	114°31'	H2566-01
<i>Squalus mitsukurini</i> Jordan and Snyder, 1903	3		220	670	24°51'	112°07'	33°19'	114°32'	H2564-01
<i>Squalus</i> sp. C (of Last and Stevens, 1994)	1		300	300	23°25'	113°04'	23°25'	113°04'	H2014-01
<i>Squalus</i> sp. D (of Last and Stevens, 1994)	1		209	478	21°39'	113°58'	27°23'	112°52'	H2547-06
<i>Squalus</i> sp. E (of Last and Stevens, 1994)	1		312	508	25°08'	112°09'	31°55'	115°10'	H2032-01
<i>Zameus squamulosus</i> (Gunther, 1877)	1		854	1254	20°08'	112°55'	32°35'	114°27'	H2560-03
PRISTIOPHORIDAE									
<i>Pristiophorus cirratus</i> (Latham, 1794)	3		203	400	30°00'	114°28'	33°24'	114°31'	H2620-05
SQUATINIDAE									
<i>Squatina tergocellata</i> McCulloch, 1914	1		203	400	29°16'	113°57'	33°24'	114°31'	H3053-02
<i>Squatina</i> sp. B (of Last and Stevens, 1994)	1		312	312	25°08'	112°09'	25°08'	112°09'	H2567-01
NARCINIDAE									
<i>Narcine</i> sp. B (of Last and Stevens, 1994)	1		209	346	21°39'	113°58'	32°05'	115°09'	H3054-03
<i>Torpedo macneilli</i> (Whitley, 1932)	1		490	490	29°21'	113°58'	29°21'	113°58'	H2591-06
RAJIDAE									
<i>Notoraja</i> sp. C (of Last and Stevens, 1994)	1		508	690	26°15'	112°03'	26°36'	112°29'	H2573-02
<i>Pavoraja allenii</i> McEachran and Fecchhelm, 1982	1		200	475	24°51'	112°07'	31°55'	115°10'	H3015-02
<i>Pavoraja</i> sp. B (of Last and Stevens, 1994)	1		520	1500	21°54'	113°41'	31°16'	114°50'	H2603-03
<i>Raja gudgeri</i> (Whitley, 1940)	1		468	490	29°21'	113°58'	33°18'	114°31'	H2519-02
<i>Raja</i> sp. E (of Last and Stevens, 1994)	1		203	362	32°10'	115°08'	33°24'	114°31'	H2619-02
<i>Raja</i> sp. F (of Last and Stevens, 1994)	1		200	510	26°43'	112°41'	32°02'	115°09'	H2570-01
<i>Raja</i> sp. I (of Last and Stevens, 1994)	1		1254	1254	25°52'	111°27'	25°52'	111°27'	H2611-02
<i>Raja</i> sp. N (of Last and Stevens, 1994)	1		203	490	27°09'	112°45'	33°24'	114°31'	H2591-01
ANACANTHOBATIDAE									
<i>Anacanthobatis</i> sp. A (of Last and Stevens, 1994)	1		482	1115	22°60'	113°14'	25°41'	111°31'	H2557-01
<i>Anacanthobatis</i> sp. C	1		1115	1158	21°54'	113°41'	25°41'	111°31'	H2569-02

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude longitude	Max. latitude longitude	Registration number
<i>Halosaurus oenii</i> Johnson, 1863	3	*	690	690	26°15'	112°03'	H2573-20
<i>Halosauropsis macrochir</i> (Günther, 1878)	3		948	948	35°25'	117°21'	H3008-03
NOTACANTHIDAE							
<i>Notacanthus sexspinis</i> Richardson, 1846	2		870	982	33°18'	114°13'	photo
ARGENTINIDAE							
<i>Glossanodon</i> sp. A	3		255	438	25°08'	112°09'	H2597-01
LEPTOCHILICHTHYIDAE							
<i>Leptoichthys microlepis</i> Machida and Shioagaki, 1988	1	*	1139	1158	20°55'	112°51'	H2544-23
ALEPOCEPHALIDAE							
<i>Alepocephalus australis</i> Barnard, 1923	1	*	982	1030	33°18'	114°13'	H3017-02
<i>Alepocephalus oustoni</i> Tanaka, 1908	1	*	880	960	22°47'	112°55'	H3061-01
<i>Alepocephalus triangularis</i> Okamura and Kawamishi, 1984	1	*	1022	1132	21°28'	113°39'	H2541-11
<i>Alepocephalus cf productus</i> (Gill, 1890)	3	*	1030	1280	20°55'	112°51'	H2544-18
<i>Baicalifornia calcarata</i> (Weber, 1913)	1	*	880	880	22°47'	113°13'	H2553-02
<i>Bathyroctes squamosus</i> Alcock, 1890	1	*	913	1139	20°16'	113°13'	H2541-10
<i>Conocara microlepis</i> (Lloyd, 1909)	1	*	1258	1258	22°29'	113°12'	H2552-07
<i>Leptoderna affinis</i> Alcock, 1899	1	*	1280	1280	32°20'	114°29'	H2614-01
<i>Leptoderna cf retrospina</i> Fowler, 1943	3	*	913	913	20°16'	113°13'	H2541-20
<i>Leptoderna cf retrospina</i> Fowler, 1943	3	*	1139	1258	20°55'	112°51'	H2552-01
<i>Narceus lloydi</i> Fowler, 1934	1	*	913	1258	20°16'	113°13'	H2552-05
<i>Roulina atrita</i> (Vallant, 1888)	1	*	1139	1258	20°55'	112°51'	H2570-05
<i>Roulina guentheri</i> Alcock, 1892	1	*	685	1061	20°08'	112°55'	H2542-11
<i>Talismania antillarum</i> (Goode and Bean, 1896)	1		685	1009	20°08'	112°55'	H2543-04
<i>Talismania longifilis</i> (Brauer, 1902)	1		913	913	20°16'	113°13'	H2541-09
<i>Talismania mekistomena</i> Sulak, 1975	1	*	1115	1254	25°41'	111°31'	H2569-08
<i>Xenodermichthys copei</i> (Gill, 1884)	1		320	1030	21°51'	113°47'	H2549-02
PLATYTRICHTHIDAE							
<i>Maulisia acuticeps</i> Sazonov, 1976	1	*	1460	1500	21°58'	113°08'	H2551-12
<i>Maulisia microlepis</i> Sazonov and Golovan, 1976	1	*	1280	1500	20°01'	113°08'	H2614-02
PHOSICHTHYIDAE							
<i>Polymetme coryllacola</i> (Alcock, 1898)	2		411	1115	22°60'	112°13'	H3035-01
ATELEOPODIDAE							
<i>Ateleopus cf japonicus</i> Bleeker, 1853	3		457	684	26°40'	112°33'	H2019-01
AULOPIIDAE							
<i>Aulopus purpurissatus</i> Richardson, 1843	2		210	210	33°45'	114°28'	H2054-01

CHLOROPHTHALMIDAE								
<i>Chlorophthalmus nigripinnis</i> Günther, 1878	2	220	727	28°48'	113°37'	35°02'	115°02'	H2590-01
<i>Chlorophthalmus cf acutifrons</i> Hiyama, 1940	3	320	467	21°38'	113°56'	24°51'	112°07'	H2103-01
<i>Chlorophthalmus cf nigromarginatus</i> Kamohara, 1953	3	328	328	21°37'	113°56'	21°37'	113°56'	H2546-04
<i>Chlorophthalmus</i> sp. A	2	328	510	21°38'	113°56'	27°17'	112°45'	H2100-01
<i>Chlorophthalmus</i> sp. B	2	200	346	21°39'	113°58'	26°45'	112°37'	H2566-02
<i>Chlorophthalmus</i> sp. C	2	200	670	26°36'	112°29'	32°10'	115°03'	H2574-02
IPNOPIDAE								
<i>Bathypterois guentheri</i> Alcock, 1889	2	868	1500	20°08'	112°55'	24°30'	111°51'	H2542-13
<i>Bathypterois ventralis</i> Garman, 1899	2	690	1500	20°16'	113°13'	27°33'	112°15'	H2544-13
<i>Bathypterois gallator</i> (Goode and Bean, 1886)	3	1460	1500	22°01'	113°08'	22°01'	113°08'	I.31151-002
SYNODONTIDAE								
<i>Bathysaurus ferox</i> Günther, 1878	2	945	1104	27°33'	112°15'	35°07'	115°01'	H3006-01
<i>Saurida longimanus</i> Norman, 1939	3	297	297	23°25'	113°04'	23°25'	113°04'	—
<i>Saurida tumbil</i> (Bloch, 1795)	3	200	320	21°39'	113°58'	26°43'	112°41'	H2547-18
<i>Saurida</i> sp. 2 (of Sainsbury <i>et al.</i> , 1985)	3	244	244	32°06'	115°10'	32°06'	115°10'	H3096-03
NEOSCOPELIDAE								
<i>Neoscopelus macrolepidotus</i> Johnson, 1863	1	435	1022	20°08'	112°55'	35°05'	114°60'	H2563-01
<i>Neoscopelus</i> sp. A	2	612	690	21°51'	113°47'	30°17'	114°30'	H3089-01
VELIFERIDAE								
<i>Velifer multiradiatus</i> Regan, 1907	2	210	210	28°09'	113°17'	28°09'	113°17'	H2020-01
POLYMIXIIDAE								
<i>Polymixia japonicus</i> Günther, 1877	2	300	510	22°60'	113°14'	30°00'	114°28'	H2554-03
<i>Polymixia</i> sp. B	2	444	467	24°51'	112°07'	24°53'	112°08'	H2565-09
MORIDAE								
<i>Antimora rostrata</i> (Günther, 1978)	1	825	1500	22°01'	113°08'	34°57'	114°29'	I.31159-003
<i>Euclichthys polyneumus</i> McCulloch, 1926	1	306	571	24°51'	112°07'	33°18'	114°31'	H3045-07
<i>Halargyreus johnsonii</i> Günther, 1862	1	843	843	35°26'	117°25'	35°26'	117°25'	H3002-01
<i>Laemonema</i> sp. A	3	982	982	33°18'	114°13'	33°18'	114°13'	H2617-01
<i>Lepidon inosiniae</i> (Günther, 1887)	2	945	945	35°07'	115°01'	35°07'	115°01'	H3010-10
<i>Lepidon microcephalus</i> Cowper, 1956	2	843	843	35°26'	117°25'	35°26'	117°25'	H3007-06
<i>Lepidon cf schmidtii</i> Svetovidov, 1936	3	785	800	35°03'	114°55'	35°03'	114°55'	H3102-01
<i>Mora moro</i> (Risso, 1810)	2	673	989	33°26'	114°21'	35°05'	115°00'	—
<i>Physiculus cf longifilis</i> Weber, 1913	3	320	320	21°45'	113°52'	21°45'	113°52'	H2548-07
<i>Physiculus cf luminosa</i> Paulin, 1983	3	320	508	26°36'	112°29'	31°55'	115°10'	H2574-08
<i>Physiculus cf nigrescens</i> Smith and Radcliffe, 1912	3	320	320	21°45'	113°52'	21°45'	113°52'	H2084-01
<i>Physiculus cf roseus</i> Alcock, 1891	3	290	320	21°45'	113°52'	21°45'	113°52'	H2548-06
<i>Tripteryphycis gilchristi</i> Boulenger, 1902	3	571	770	26°15'	112°03'	35°02'	115°02'	H2596-02
BREGMACEROTIDAE								
<i>Bregmaceros</i> sp. A	1	413	413	29°50'	114°21'	29°50'	114°21'	H3029-04
MELANONIIDAE								
<i>Melanonus zugmayeri</i> Norman, 1903	2	880	913	20°16'	113°13'	20°16'	113°13'	H3110-02

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude	Min. longitude	Max. latitude	Max. longitude	Registration number
MERLUCCIIDAE									
<i>Macrurus novaezelandiae</i> (Hector, 1871)	1		596	825	33°06'	114°30'	34°15'	114°20'	H3025-07
OPHIIDIIDAE									
<i>Bassozetus</i> sp. A	3	*	1460	1500	22°01'	113°08'	22°01'	113°08'	H2551-01
<i>Dannevigia tusca</i> Whitley, 1941	2		203	390	28°53'	113°41'	33°24'	114°31'	H3052-01
<i>Dicrolene</i> sp. A	2		435	945	25°59'	112°38'	30°52'	114°37'	H2583-11
<i>Dicrolene</i> sp. B	2	*	1158	1158	21°54'	113°41'	21°54'	113°41'	H2550-06
<i>Epetriodus freddyi</i> Cohen and Nielsen, 1978	2	*	714	892	24°30'	111°51'	27°07'	112°23'	H2562-02
<i>Eretmichthys</i> sp. A	3	*	1460	1500	21°50'	113°59'	21°50'	113°59'	H2559-09
<i>Gemypterus blacodes</i> (Forster, 1801)	1		596	989	33°06'	114°30'	35°05'	114°53'	H3178-02
<i>Glyptothidium japonicum</i> Kamohara, 1936	2		437	478	26°40'	112°33'	27°49'	113°01'	H2575-05
<i>Hoplobrotula armata</i> (Temminck and Schlegel, 1847)	3		320	438	21°45'	113°52'	27°09'	112°45'	H2578-11
<i>Homostolus acer</i> Smith and Radcliffe, 1913	2	*	612	612	23°44'	112°35'	23°44'	112°35'	H2558-02
<i>Lampragannus cf niger</i> Alcock, 1891	3	*	868	868	20°08'	112°55'	20°08'	112°55'	H2542-01
<i>Monomitopus</i> sp. A	2		868	1258	20°08'	112°55'	32°35'	114°27'	H2615-03
<i>Monomitopus</i> sp. B	2	*	1254	1254	25°52'	111°27'	25°52'	111°27'	H2544-15
<i>Monomitopus</i> sp. C	2	*	1254	1254	25°52'	111°27'	25°52'	111°27'	H2570-11
<i>Porogadus</i> sp. A	4	*	1104	1104	27°33'	112°15'	27°33'	112°15'	H2582-01
<i>Xyelacyba niyersi</i> Cohen, 1961	2	*	1158	1158	21°54'	113°41'	21°54'	113°41'	H2550-07
Ophidiidae gen. sp.	4	*	913	913	20°16'	113°13'	20°16'	113°13'	H2541-08
BYTHITIDAE									
<i>Diplacanthopoma</i> sp. A	2	*	868	868	20°08'	112°55'	20°08'	112°55'	H2542-22
CARAPIIDAE									
<i>Pyramodon ventralis</i> Smith and Radcliffe, 1913	2		346	510	25°36'	112°33'	33°18'	114°31'	I.31174-008
MACROURIDAE									
<i>Bathygadus cottoides</i> Günther, 1878	1		913	1280	20°16'	113°13'	34°10'	114°16'	H2571-02
<i>Bathygadus</i> sp. A	3	*	1030	1030	34°10'	114°16'	34°10'	114°16'	H3017-08
<i>Caelorinchus acanthiger</i> Barnard, 1925	1	*	510	1132	27°17'	112°45'	35°05'	114°60'	H3008-08
<i>Caelorinchus imnotabilis</i> McCulloch, 1907	1		770	1030	29°52'	114°12'	35°05'	114°60'	H3007-10
<i>Caelorinchus matalama</i> (McCann and McKnight, 1980) 1		870	870	35°05'	114°60'	35°05'	114°60'	H3008-09	
<i>Caelorinchus muraufasciatus</i> McMillan and Paulin, 1993	1		320	714	26°15'	112°03'	35°02'	115°02'	H2604-10
<i>Caelorinchus muraufasciatus</i> McMillan and Paulin, 1993 1	1		306	510	24°53'	112°08'	32°54'	114°39'	H3028-03
<i>Caelorinchus parvifasciatus</i> McMillan and Paulin, 1993 1	3	390	475	31°17'	114°53'	33°18'	114°31'	H2604-02	
<i>Caelorinchus cf argenteatus</i> (Smith and Radcliffe, 1912)			320	320	21°45'	113°13'	21°45'	113°52'	H2305-02
<i>Caelorinchus</i> sp. A	1	*	390	475	31°17'	114°53'	33°18'	114°31'	H2604-02
<i>Caelorinchus</i> sp. C	1	*	482	612	22°60'	113°14'	23°45'	112°35'	H1514-19
<i>Caelorinchus</i> sp. D	1	*	685	685	21°51'	113°47'	21°51'	113°47'	H2549-04
<i>Caelorinchus</i> sp. E	1	*	478	1104	22°60'	113°14'	30°17'	114°30'	H2024-01
<i>Caelorinchus</i> sp. F	1	*	685	1022	21°28'	113°39'	24°31'	111°50'	H2553-03

<i>Caelornichus</i> sp. G	1	*	1030	1030	32°35'	114°27'	32°35'	114°27'	H2615-02
<i>Cetoniichthys subinflatus</i> Sazonov and Shcherbachev, 1982	1	*	1258	1258	22°29'	113°12'	22°29'	113°12'	H2551-13
<i>Cetoururus globiceps</i> (Vaillant, 1884)	1		740	1500	22°01'	113°08'	34°13'	114°08'	H2551-15
<i>Coryphaenoides nudis</i> Günther, 1878	1	*	982	982	33°18'	114°13'	33°18'	114°13'	H2617-02
<i>Coryphaenoides serrulatus</i> Günther, 1878	1		740	982	32°40'	114°28'	35°05'	114°60'	H2616-02
<i>Coryphaenoides striatulus</i> Barnard, 1925	1	*	982	1030	33°18'	114°13'	34°10'	114°16'	H3017-06
<i>Coryphaenoides</i> sp. A	1	*	945	1030	32°35'	114°27'	35°07'	115°01'	H3010-09
<i>Coryphaenoides</i> sp. B	1	*	1254	1500	22°01'	113°08'	25°52'	111°27'	H2561-03
<i>Gadomus</i> sp. A	1		320	1158	21°51'	113°47'	31°55'	115°10'	H2596-03
<i>Gadomus</i> sp. B	1		817	1500	20°08'	112°55'	34°15'	114°20'	H3001-01
<i>Hymenocephalus adelscottii</i> Iwamoto and Merrett, 1996	2	*	430	690	17°45'	118°32'	26°15'	112°03'	H2573-14
<i>Hyomacurus</i> sp. A	2		685	685	21°51'	113°47'	21°51'	113°47'	H2549-13
<i>Idiolphorhynchus andriashevi</i> Sazonov, 1981	1		1240	1240	34°13'	114°08'	34°13'	114°08'	H2623-01
<i>Kuronezumia leonis</i> (Barnard, 1925)	1	*	842	842	35°25'	117°21'	35°25'	117°21'	H3008-10
<i>Kuronezumia pallida</i> Sazonov and Iwamoto, 1992	2	*	760	760	26°36'	112°09'	26°36'	112°09'	H3041-14
<i>Lepidiorhynchus deniculatus</i> (Richardson, 1846)	1		320	817	22°60'	113°14'	35°02'	115°02'	H2023-01
<i>Lucigadus ori</i> (Smith, 1968)	1	*	666	738	26°57'	112°22'	34°59'	114°44'	H2579-02
<i>Malacocephalus laevis</i> (Lowe, 1843)	1		411	870	22°60'	113°14'	34°59'	114°44'	H2023-05
<i>Matteocephalus acipenserinus</i> (Gilbert and Cramer, 1897)	2	*	685	945	20°08'	112°55'	29°22'	113°47'	H2542-30
<i>Nezumia evrides</i> Gilbert and Hubbs, 1920	1	*	612	913	20°16'	113°13'	25°19'	111°56'	H2549-17
<i>Nezumia spinosa</i> (Gilbert and Hubbs, 1916)	1		685	1258	20°08'	112°55'	29°22'	113°47'	H1492-01
<i>Nezumia</i> sp. A	1	*	320	1009	26°15'	112°03'	32°02'	114°54'	H2573-12
<i>Nezumia</i> sp. B	1	*	714	945	27°07'	112°23'	28°04'	112°43'	H2580-04
<i>Nezumia</i> sp. C	1	*	1293	1500	22°01'	113°08'	24°10'	111°39'	H2551-17
<i>Nezumia</i> sp. D	1	*	685	1258	20°55'	112°51'	33°18'	114°13'	H3041-12
<i>Nezumia</i> sp. E	1	*	842	945	28°00'	112°41'	35°25'	117°21'	H3008-11
<i>Pseudonezumia puscilla</i> Sazonov and Shcherbachev, 1981	1	*	1460	1500	22°01'	113°08'	22°01'	113°08'	H2551-19
<i>Sphagiennacurus pumiliceps</i> (Alcock, 1894)	1	*	882	1500	22°01'	113°08'	33°18'	114°13'	H2617-03
<i>Trachonurus</i> sp. A	2	*	892	1030	24°30'	111°51'	34°10'	114°16'	H3002-05
<i>Trachonurus</i> sp. B	2	*	770	1132	20°08'	112°55'	32°40'	114°28'	H2596-04
<i>Trachonurus</i> sp. C	2	*	770	1293	20°16'	113°13'	34°13'	114°08'	H2596-01
<i>Ventrifossa johnbaborum</i> Iwamoto, 1982	1	*	684	882	20°08'	112°55'	30°17'	114°30'	H2573-21
<i>Ventrifossa macropogon</i> Marshall, 1973	1	*	320	760	21°51'	113°47'	33°26'	114°21'	H2549-09
<i>Ventrifossa nigrodorsalis</i> Gilbert and Hubbs, 1920	1		482	901	23°00'	113°14'	24°32'	111°49'	H2554-11
<i>Ventrifossa</i> sp. A	1	*	482	714	21°51'	113°47'	28°06'	113°27'	H2580-03
<i>Ventrifossa</i> sp. B	1	*	780	817	33°26'	114°21'	33°25'	114°23'	—
LOPHIIDAE									
<i>Lophioides</i> sp. A	3		300	300	23°52'	113°04'	23°25'	113°04'	—
<i>Lophiomus setigerus</i> (Vahl, 1797)	2		250	612	21°45'	113°52'	32°14'	115°06'	H3056-04
<i>Sladenia</i> sp. A	3	*	1139	1158	20°55'	112°51'	24°00'	111°54'	H2544-02
CHAUNACIDAE									
<i>Bathychaunax melanostomus</i> Caruso, 1989	2		893	1500	20°55'	112°51'	30°52'	114°37'	H2551-03
<i>Chaunax cf. fimbriatus</i> Hügendorf, 1879	3	*	320	1060	21°38'	113°56'	33°23'	114°30'	H2565-13
<i>Chaunax</i> sp. A	3	*	380	510	30°00'	114°28'	32°02'	115°09'	H2611-01
<i>Chaunax</i> sp. B	3	*	444	444	24°53'	112°08'	24°53'	112°08'	H2565-14

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude	Min. longitude	Max. latitude	Max. longitude	Registration number
OGCOCEPHALIDAE									
<i>Coelophrys</i> sp. A	3	*	1009	1139	20°55'	112°51'	27°22'	112°11'	H2544-07
<i>Dibranchius</i> sp. A	3	*	297	297	23°25'	113°04'	23°25'	113°04'	H2555-01
<i>Halieuteta cf stellata</i> (Vahl, 1797)	3	*	435	1115	24°53'	113°13'	27°17'	112°45'	H3040-10
<i>Halieutopsis cf micropus</i> (Alcock, 1891)	3	*	942	942	29°22'	113°47'	29°22'	113°47'	H2593-01
<i>Halieutopsis</i> sp. A	3	*	942	942	29°22'	113°47'	29°22'	113°47'	H2592-05
BARBOURISIIDAE									
<i>Barbourisia rufa</i> Parr, 1945	1		1139	1460	20°55'	112°51'	24°10'	111°39'	H2551-02
DIRETMIDAE									
<i>Diretmichthys parini</i> (Post and Quero, 1981)	2		740	1293	20°55'	112°51'	35°02'	115°01'	H3009-01
<i>Diretmus argenteus</i> Johnson, 1864	2		685	1139	20°08'	112°55'	21°51'	113°47'	H2542-07
TRACHICHTHYIDAE									
<i>Gephyroberyx darwinii</i> (Johnson, 1866)	2		274	490	21°44'	113°52'	33°13'	114°31'	H2044-01
<i>Hoplostethus atlanticus</i> Collett, 1889	1		812	870	33°58'	114°22'	35°05'	114°60'	H1251-01
<i>Hoplostethus intermedius</i> (Hector, 1875)	1		673	673	35°02'	115°02'	35°02'	115°02'	H3011-03
<i>Hoplostethus latius</i> McCulloch, 1914	1	*	320	510	24°53'	112°08'	33°18'	114°31'	H3023-06
<i>Hoplostethus cf melanopus</i> (Weber, 1913)	3	*	435	760	18°14'	117°54'	27°07'	112°23'	H3041-01
BERYCIDAE									
<i>Beryx splendens</i> Lowe, 1833	2		209	670	21°38'	113°56'	32°02'	114°54'	H2599-02
<i>Centroberyx australis</i> Shimizu and Hutchins, 1987	2		203	380	26°42'	112°38'	33°24'	114°31'	H2577-01
<i>Centroberyx gerrardi</i> (Günther, 1887)	2		210	210	33°45'	114°28'	33°45'	114°28'	H2008-01
HOLOCENTRIDAE									
<i>Ostichthys japonicus</i> (Cuvier, 1829)	2		200	225	21°39'	113°58'	26°43'	112°41'	H2576-04
PARAZENIDAE									
<i>Parazen pacificus</i> Kamohara, 1935	2		297	478	21°45'	113°52'	27°23'	112°52'	H3045-03
MACROUROCYTTIDAE									
<i>Zenion</i> sp. A	3		306	735	21°45'	113°52'	27°23'	112°52'	H3040-01
ZEIDAE									
<i>Cyttopsis cypho</i> (Fowler, 1934)	2		297	510	21°45'	113°52'	32°02'	115°09'	H2556-08
<i>Cyttopsis roseus</i> (Lowe, 1843)	2		209	616	21°39'	113°58'	29°50'	114°21'	H2591-04
<i>Cyttus traversi</i> Hutton, 1872	1		490	1003	28°13'	113°07'	35°08'	115°01'	H3009-02
<i>Zenopsis nebulosus</i> (Temminck and Schlegel, 1845)	1		209	712	21°39'	113°58'	34°59'	114°53'	H2040-01
<i>Zenopsis</i> sp. A	2		209	392	16°54'	120°25'	21°45'	113°52'	H2046-01
<i>Zen</i> <i>faber</i> Linnaeus, 1758	1		200	230	26°43'	112°41'	32°00'	115°13'	H2576-05
GRAMMICOLEPIDIDAE									
<i>Grammicolepis brachiusculus</i> Poey, 1873	2		565	612	25°19'	111°56'	26°25'	112°20'	H3046-04
<i>Xenolepidichthys dalelshii</i> Gilchrist, 1922	2		405	612	17°00'	120°11'	31°31'	114°43'	H2079-01

Oreosomatidae

<i>Alloctylus verrucosus</i> (Gilchrist, 1906)	1	613	1293	20°08'	112°55'	35°05'	114°60'	H2036-01
<i>Neocyttus rhomboidalis</i> Gilchrist, 1906	1	596	1240	26°36'	112°09'	35°05'	114°60'	H2034-01
<i>Oreosoma atlanticum</i> Cuvier, 1829	1	670	825	32°02'	114°54'	34°15'	114°20'	H3016-01
<i>Pseudocyttus maculatus</i> Gilchrist, 1906	1	900	1003	35°03'	115°01'	35°08'	114°51'	H3008-01

Caproidae

<i>Antigonia rhomboides</i> McCulloch, 1915	2	297	435	22°30'	113°35'	25°36'	112°10'	H3045-04
<i>Antigonia rubicunda</i> Ogilby, 1910	2	312	312	25°08'	112°09'	25°08'	112°09'	H2567-17

Fistulariidae

<i>Fistularia petimba</i> Lacépède, 1803	2	218	218	27°33'	112°59'	27°33'	112°59'	P.30431-001
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Macroramphosidae

<i>Centriscoptes humerosus</i> (Richardson, 1846)	2	306	673	27°23'	112°52'	35°02'	115°02'	H3071-01
<i>Macroramphosus scolopax</i> (Linnaeus, 1758)	2	225	308	23°25'	113°04'	32°14'	115°06'	I.31185-009
<i>Notopogon xenosoma</i> Regan, 1914	2	270	712	24°51'	112°07'	34°59'	114°53'	H2567-04

Scorpaenidae

<i>Helicolenus barathri</i> (Hector, 1875)	2	320	770	26°36'	112°29'	33°18'	114°31'	H2574-01
<i>Helicolenus cf. percooides</i> (Richardson, 1842)	3	203	225	32°10'	115°08'	33°24'	114°31'	H2613-03
<i>Neomerinthe cf. nelsoni</i> (Smith, 1964)	3	320	438	27°09'	112°45'	31°55'	115°10'	I.31184-004
<i>Neosebastes nigropunctatus</i> McCulloch, 1915	2	203	225	32°10'	115°08'	33°24'	114°31'	H2613-07
<i>Neosebastes pandius</i> (Richardson, 1842)	2	201	201	34°57'	114°56'	34°57'	114°56'	H3063-01
<i>Neosebastes thetidis</i> (Waite, 1899)	2	203	225	32°10'	115°08'	33°24'	114°31'	H2613-08
<i>Setarches guntheri</i> Johnson, 1862	2	318	649	17°50'	118°33'	30°57'	114°48'	H2006-02
<i>Setarches longimanus</i> (Alcock, 1894)	2	297	297	23°25'	113°04'	23°25'	113°04'	I.31155-008
<i>Trachyscorpia capensis</i> (Gilchrist and von Bonde, 1924)	2	738	870	34°59'	114°44'	35°05'	114°60'	H2625-02
<i>Trachyscorpia cf. cristulata</i> (Goode and Bean, 1896)	3	880	880	32°40'	114°28'	32°40'	114°28'	H2616-01

Triglidae

<i>Heminodus</i> sp. A	3	297	508	22°60'	113°14'	27°09'	112°45'	H2564-13
<i>Lepidotrigla modesta</i> Waite, 1899	1	270	308	32°05'	115°09'	32°14'	115°06'	H2609-01
<i>Lepidotrigla</i> sp. A	2	209	346	21°39'	113°58'	29°16'	113°57'	H2547-07
<i>Lepidotrigla</i> sp. B	2	320	320	21°39'	113°58'	25°08'	113°09'	H2547-08
<i>Parapterygotrigla</i> sp. A	2	297	300	23°25'	113°04'	23°25'	113°04'	H2555-05
<i>Parapterygotrigla</i> sp. B	3	300	300	23°25'	113°04'	23°25'	113°04'	H2556-10
<i>Peristichion cf. liorhynchus</i> (Günther, 1872)	3	297	467	23°25'	113°04'	24°56'	112°11'	H2564-10
<i>Pterygotrigla hemisticta</i> (Temminck and Schlegel, 1844)	2	300	320	21°45'	113°52'	23°25'	113°04'	H2548-11
<i>Pterygotrigla polyommata</i> (Richardson, 1839)	3	203	400	30°01'	114°29'	33°24'	114°31'	H2597-04
<i>Satyricthys cf. adeni</i> (Lloyd, 1907)	4	444	444	24°53'	112°08'	24°53'	112°08'	H2115-01
<i>Satyricthys cf. investigatoris</i> (Alcock, 1898)	3	320	714	26°15'	112°03'	31°55'	115°10'	H2608-03
<i>Satyricthys cf. murrayi</i> (Günther, 1878)	4	297	300	23°25'	113°04'	23°25'	113°04'	H2555-07
<i>Satyricthys cf. wuelchi</i> (Herre, 1925)	4	209	346	21°39'	113°58'	32°05'	115°09'	H2547-05

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min.		Max.		Registration number
					latitude	longitude	latitude	longitude	
PLATYCEPHALIDAE									
<i>Bembras</i> sp. A	2		209	297	21°39'	113°58'	23°25'	113°04'	H2547-04
<i>Elates ransonnetii</i> (Steindachner, 1877)	3		221	221	22°22'	113°39'	22°22'	113°39'	H3055-02
<i>Neoplatycephalus conatus</i> Waite and McCulloch, 1915	1		201	413	28°53'	113°41'	33°24'	114°31'	H2610-08
<i>Ratabulus diversidens</i> (McCulloch, 1914)	2		209	209	21°39'	113°58'	21°39'	113°58'	H2547-15
HOPLICHTHYIDAE									
<i>Hoplichthys citrinus</i> Gilbert, 1905	2		300	612	23°25'	113°04'	27°09'	112°45'	H3045-09
<i>Hoplichthys hasuelli</i> McCulloch, 1907	1		373	712	29°21'	113°58'	34°59'	114°53'	H1807-01
<i>Hoplichthys</i> sp. A	3		510	1058	30°39'	114°28'	34°59'	114°53'	H2601-01
EREUNIIDAE									
<i>Ereunias cf gallator</i> Jordan and Snyder, 1901	3	*	565	760	26°25'	112°20'	28°13'	113°07'	I.31175-001
PSYCHROLUTIDAE									
<i>Psychrolutes cf inermis</i> (Vaillant, 1888)	3		435	565	26°25'	112°20'	26°25'	112°20'	H3046-05
<i>Psychrolutes cf marcidus</i> (McCulloch, 1926)	3		571	945	26°15'	112°03'	32°52'	114°35'	H3026-01
CYCLOPTERIDAE									
<i>Paraliparis</i> sp. A	3		1030	1030	32°35'	114°27'	32°35'	114°27'	H2615-10
DACTYLOPTERIDAE									
<i>Dactyloptena peterseni</i> (Nyström, 1887)	3		250	250	27°29'	112°50'	27°29'	112°50'	H3066-03
SERRANIIDAE									
<i>Callanthis</i> sp. A	2	*	203	270	27°39'	113°00'	33°24'	114°31'	H2610-01
<i>Caprodon</i> sp. A	2	*	212	373	22°22'	113°39'	32°54'	114°39'	H2307-01
<i>Epinephelus radiatus</i> (Day, 1868)	2		218	250	21°19'	113°42'	22°30'	113°35'	—
<i>Epinephelus septemfasciatus</i> (Thunberg, 1793)	2		200	331	31°09'	114°52'	32°09'	115°10'	H2130-01
<i>Lepidoperca filamenta</i> Roberts, 1987	2		203	225	32°10'	115°08'	33°24'	114°31'	H2613-05
<i>Lepidoperca occidentalis</i> Whitley, 1951	2		203	225	32°10'	115°08'	33°24'	114°31'	H2613-04
<i>Plectranthias cf japonicus</i> (Steindachner, 1884)	3		320	320	21°45'	113°52'	21°45'	113°52'	H2548-02
GLAUCOSOMATIDAE									
<i>Glaucosoma buergeri</i> Richardson, 1845	2		220	250	22°25'	113°37'	22°29'	113°36'	P.30423-001
BANJOSIIDAE									
<i>Banjios banjos</i> (Richardson, 1846)	2		216	216	28°34'	113°29'	28°34'	113°29'	H2037-02
PRIACANTHIDAE									
<i>Cookeolus boops</i> (Forster, 1801)	2		200	300	23°25'	113°04'	27°53'	113°08'	H2575-03
<i>Priacanthus hamrur</i> (Forsskal, 1775)	2		218	250	21°19'	113°42'	22°30'	113°35'	—
<i>Priacanthus macracanthus</i> Cuvier, 1829	2		209	320	21°39'	113°58'	21°39'	113°58'	H2085-01
<i>Priacanthus fitchi</i> Starnes, 1988	2		297	297	23°25'	113°04'	23°25'	113°04'	—
<i>Pristigeynus niphonia</i> (Cuvier, 1829)	2		220	250	22°25'	113°37'	22°29'	113°36'	—

EPITOGONIDAE									
<i>Epigonus macrops</i> (Brauer, 1906)	2	612	895	24°30'	111°51'	25°19'	111°56'	H2562-01	
<i>Epigonus occidentalis</i> Goode and Bean, 1896	3	612	613	23°45'	112°35'	31°16'	114°50'	H2603-01	
<i>Epigonus robustus</i> (Barnard, 1927)	2	976	982	33°17'	114°13'	33°18'	114°13'	H2617-10	
ACROPOMATIDAE									
<i>Acropoma japonica</i> Günther, 1859	3	209	320	21°39'	113°58'	27°23'	112°52'	H2547-12	
<i>Apoogonops anomalus</i> Ogilby, 1896	2	200	510	21°45'	113°52'	33°18'	114°31'	—	
<i>Doderleinia beryoides</i> (Hilgendorf, 1879)	2	320	400	20°00'	120°14'	21°45'	113°52'	H2548-03	
<i>Malakichthys cf. elegans</i> Matsubara and Yamaguchi, 1943	3	320	320	21°45'	113°52'	21°45'	113°52'	H2088-01	
<i>Malakichthys</i> sp. A	3	297	482	22°60'	113°14'	27°23'	112°52'	H2554-15	
<i>Polypriion americanus</i> (Bloch and Schneider, 1801)	2	270	270	32°05'	115°09'	32°05'	115°09'	—	
<i>Polyprion oxygeneus</i> (Forster, 1801)	2	350	350	32°18'	114°58'	32°18'	114°58'	photo	
<i>Synagrops japonicus</i> (Döderlein, 1884)	2	306	714	22°60'	113°14'	32°10'	115°03'	H2047-01	
<i>Synagrops philippinensis</i> (Günther, 1880)	2	306	478	21°45'	113°52'	30°00'	114°28'	—	
MALACANTHIDAE									
<i>Branchistegus australiensis</i> Dooley and Kailola, 1988	2	207	230	20°40'	113°43'	32°00'	115°13'	H2547-03	
EMMELICHTHYIDAE									
<i>Plagiogonion macrolepis</i> McCulloch, 1914	3	203	230	32°00'	115° 13'	33°24'	114°31'	H2619-04	
LUTJANIDAE									
<i>Etelis carbunculus</i> Cuvier, 1828	1	200	285	21°15'	113°43'	26°24'	112°38'	H2577-03	
<i>Etelis coruscans</i> Valenciennes, 1862	1	285	285	26°42'	112°38'	26°42'	112°38'	H2577-02	
<i>Lipocheilus carnolabrum</i> (Chan, 1970)	2	218	250	21°19'	113°42'	22°30'	113°35'	photo	
NEMIPTERIDAE									
<i>Nemipterus bathybius</i> Snyder, 1911	2	209	225	20°40'	113°43'	21°39'	113°58'	H3054-02	
<i>Parascopopsis rufomaculatus</i> Russell, 1986	2	209	312	21°39'	112°58'	25°08'	112°09'	H2567-05	
HAEMULIDAE									
<i>Haplogenyis kishinouyei</i> Smith and Pope, 1906	3	218	250	20°40'	113°43'	22°30'	113°35'	photo	
SPARIDAE									
<i>Dentex tumifrons</i> (Temminck and Schlegel, 1842)	2	200	346	21°39'	113°58'	32°10'	115°08'	H3067-02	
<i>Pagrus auratus</i> (Bloch and Schneider, 1801)	2	200	296	21°15'	113°43'	32°24'	115°01'	H1698-01	
MULLIDAE									
<i>Parupeneus chrysopleuron</i> (Schlegel, 1843)	2	200	200	26°43'	112°41'	26°43'	112°41'	I.31173-001	
BATHYCLUPEIDAE									
<i>Bathyclupea</i> sp. A	3	482	870	22°60'	113°14'	33°58'	114°22'	H3040-03	
SCORPIDIDAE									
<i>Tilodon sexfasciatus</i> (Richardson, 1842)	2	201	201	34°57'	114°56'	34°57'	114°56'	H3063-03	
CHAETODONTIDAE									
<i>Chaetodon assarius</i> Waite, 1905	2	200	250	32°00'	115°30'	32°00'	115°30'	P.30422-001	
PENTACEROTIDAE									
<i>Parisiprius gallipao</i> Whitley, 1944	2	204	213	28°03'	113°15'	31°36'	114°59'	H3068-01	

Species	ID level	New record (Aust)	Min. depth (m)	Max depth (m)	Min. latitude	Min. longitude	Max. latitude	Max. longitude	Registration number
<i>Pentaceros decacanthus</i> Günther, 1859	2		306	712	25°08'	112°09'	34°59'	114°53'	H3069-04
<i>Pseudopentaceros cf richardsoni</i> (Smith, 1844)	3		376	596	28°48'	113°37'	33°13'	114°31'	H3025-01
<i>Zanclus leucurus</i> (Ramsay and Ogilby, 1889)	2		200	360	31°55'	115°11'	33°24'	114°31'	H2002-02
OPLEGNATHIDAE									
<i>Oplegnathus woodwardi</i> (Waite, 1900)	2		203	380	29°57'	114°27'	33°24'	114°31'	H2608-05
CHEILODACTYLIDAE									
<i>Nemadactylus macropterus</i> (Bloch and Schneider, 1801)	2		203	357	31°55'	115°10'	33°24'	114°31'	H2608-14
<i>Nemadactylus valenciennesi</i> (Whitley, 1937)	2		203	203	33°24'	114°31'	33°24'	114°31'	H2619-05
CEPOLIDAE									
<i>Cepola</i> sp. A	3		300	300	23°25'	113°04'	23°25'	113°04'	H2556-01
SPHYRAENIDAE									
<i>Sphyræna</i> sp. A	3		209	300	21°39'	113°58'	23°25'	113°04'	H2547-14
LABRIDAE									
<i>Bodianus vulpinus</i> (Richardson, 1850)	1		218	218	27°33'	112°58'	27°33'	112°58'	H2065-01
PINGUIPIDAE									
<i>Parapercis</i> sp. A	3		225	390	31°55'	115°10'	32°14'	115°06'	H2608-02
<i>Parapercis</i> sp. B	3		220	318	23°25'	113°04'	33°19'	114°32'	I31185-006
<i>Parapercis</i> sp. C	3		220	297	23°25'	113°04'	33°19'	114°32'	H2556-09
PERCOPHIDAE									
<i>Benbrops cf curvatura</i> Ikada and Suzuki, 1952	3		320	320	21°45'	113°52'	21°45'	113°52'	-
URANOSCOPIDAE									
<i>Gnathagnus australiensis</i> Kishimoto, 1989	2		290	320	21°45'	113°52'	21°45'	113°52'	H2548-04
<i>Kathetostoma nigrofasciatum</i> Waite and McCulloch, 1915	2		201	320	30°01'	114°29'	34°57'	114°56'	H2597-05
<i>Pleuroscopus pseudodorsalis</i> Barnard, 1927	2		435	435	33°20'	114°30'	33°20'	114°30'	H3023-04
<i>Uranoscopus</i> sp. A	3		209	320	21°39'	113°58'	21°45'	113°52'	H2547-13
CHAMPSODONTIDAE									
<i>Champsodon cf longipinnis</i> Matsubara and Amaoka, 1964	3		297	612	22°60'	113°14'	27°17'	112°45'	H3046-01
<i>Champsodon nudivittatus</i> (Ogilby, 1895)	2		306	478	24°51'	112°07'	27°23'	112°52'	H2575-03
CALLIONYMIDAE									
<i>Synchropus apricus</i> (McCulloch, 1926)	2		390	490	27°09'	112°45'	31°49'	115°01'	H2587-03
SCOMBROLABRACIDAE									
<i>Scombrolabrax heterolepis</i> Roule, 1921	2		854	1293	20°08'	112°55'	35°07'	115°01'	H3010-05
GEMPYLIDAE									
<i>Necopecten orientalis</i> (Gilchrist and von Bonde, 1924)	1		435	510	24°51'	112°07'	27°17'	112°45'	H2564-03
<i>Rexia antefurcata</i> Parin, 1989	2		225	435	22°22'	113°39'	25°36'	112°10'	H3058-01

<i>Rexia bengalensis</i> (Alcock, 1894)	2	270	270	22°13'	113°44'	22°13'	113°44'	H3057-01
<i>Rexia promethicoides</i> (Bleeker, 1856)	1	297	320	21°45'	113°52'	23°25'	113°04'	I.31147-001
<i>Rexia solandri</i> (Cuvier, 1831)	1	216	596	23°25'	113°04'	33°20'	114°30'	H3023-05
CENTROLOPHIDAE								
<i>Hyperoglyphe antarctica</i> (Carmichael, 1818)	2	380	380	30°00'	114°28'	30°00'	114°28'	H2598-02
<i>Psenopsis obscura</i> Haedrich, 1967	2	868	868	20°08'	112°55'	20°08'	112°55'	H2543-02
NOMEIDAE								
<i>Cubiceps pauciradiatus</i> Günther, 1872	2	868	868	20°08'	112°55'	20°08'	112°55'	H2543-01
<i>Cubiceps squamiceps</i> (Lloyd, 1909)	2	467	467	24°51'	112°07'	24°51'	112°07'	H2564-23
ARIOMMATIDAE								
<i>Arionma luridum</i> Jordan and Snyder, 1904	2	297	318	23°25'	113°04'	24°56'	112°11'	—
CITHARIDAE								
<i>Citharoides macrolepidotus</i> (Gilchrist, 1905)	3	297	435	23°25'	113°04'	31°55'	115°10'	H3045-05
BOTHIDAE								
<i>Chascanopsetta lugubris</i> Alcock, 1894	2	444	467	24°51'	112°07'	24°53'	112°08'	H2564-21
<i>Taenionsetta</i> cf <i>ocellata</i> (Günther, 1880)	3	300	300	23°25'	113°04'	23°25'	113°04'	H2556-02
PARALICHTHYIDAE								
<i>Pseudorhombus megalops</i> Fowler, 1934	3	297	300	23°25'	113°04'	23°25'	113°04'	—
PLEURONECTIDAE								
<i>Poecilopsetta</i> cf <i>prolonga</i> Alcock, 1894	3	312	320	21°45'	113°52'	25°08'	112°09'	H2548-15
<i>Pleuronectidae</i> gen. sp.	4	320	320	21°45'	113°52'	21°45'	113°52'	H2567-15
TRIACANTHODIDAE								
<i>Halimochirus alcocki</i> Weber, 1913	1	438	438	27°09'	112°45'	27°09'	112°45'	I.31184-002
<i>Halimochirus centriscoides</i> Alcock, 1899	1	297	297	23°25'	113°04'	23°25'	113°04'	I.31155-003
<i>Paratriacanthodes retrospinus</i> Fowler, 193	1	467	482	22°60'	113°14'	24°51'	112°07'	I.31154-001
<i>Tydemania navigatoris</i> Weber, 1913	1	482	482	22°60'	113°14'	22°60'	113°14'	I.31154-002
MONACANTHIDAE								
<i>Eubalichthys bucephalus</i> (Whitley, 1931)	1	204	213	31°13'	114°56'	34°56'	114°59'	H1800-01
<i>Eubalichthys quadrispinis</i> Hutchins, 1977	1	213	270	31°13'	114°56'	32°10'	115°08'	H2610-04
<i>Nelusetta agraudi</i> (Quoy and Gaimard, 1824)	1	200	360	29°20'	114°02'	32°28'	114°59'	H1800-02
<i>Perika scaber</i> (Bloch and Schneider, 1801)	1	203	203	33°24'	114°31'	33°24'	114°31'	H2619-07
<i>Thamnaconus tessellatus</i> (Günther, 1880)	1	250	250	27°29'	112°50'	27°29'	112°50'	H1802-01
OSTRACIIDAE								
<i>Anaplocapros lenticularis</i> (Richardson, 1841)	2	203	324	31°12'	114°56'	33°24'	114°31'	H2613-09
<i>Capropygia unistriata</i> (Kaup, 1855)	2	203	203	33°24'	114°31'	33°24'	114°31'	—
TETRAODONTIDAE								
<i>Omegophora armilla</i> (McCulloch and Waite, 1915)	2	255	255	30°01'	114°29'	30°01'	114°29'	I.31186-002
<i>Sphaeroides pachygaster</i> (Müller and Troschel, 1848)	3	318	685	21°51'	113°47'	24°56'	112°11'	H2566-03

The birds of Sumbawa, Moyo and Sangeang Islands, Nusa Tenggara, Indonesia

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Abstract – This paper is based mainly on data gathered during a vertebrate survey of Sumbawa, Moyo and Sangeang Islands by a joint Western Australian Museum–Museum Zoologicum Bogoriense expedition in May and October–November 1988, a Cambridge student expedition to Sumbawa Island in July–August 1993; and a visit by P. Jepson and S. Schmitt to Sumbawa in September 1993.

A total of 172 species of bird were recorded and 362 specimens were collected which include the first major collections from Moyo and Sangeang Islands and represent important new collections for Sumbawa Island. The local distribution, abundance and habitat preferences found for each species are described. Many specimens and observations represent new island and/or archipelago records.

INTRODUCTION

The islands of Sumbawa, Moyo and Sangeang lie in the inner Banda arc of the Indonesian archipelago between longitude 116°45' and 119°15' east and latitude 8°0' and 9°15' south. They are situated between Lombok in the west and Komodo and Flores in the east in the Indonesian province of Nusa Tenggara Barat (Figure 1). The Flores Sea is to the north and the Indian Ocean to the south. The major aim of this work was to document the distribution and status of the avifauna of Sumbawa, Moyo and Sangeang Islands and to collect series of certain species for taxonomic, morphological and genetic studies. The islands were visited by the joint Western Australian Museum–Museum Zoologicum Bogoriense group between 6–28 May and 18 October to 15 November 1988. Additional information was collated from the Cambridge Flores–Sumbawa expedition carried out between 28 July and 19 August 1993 by Butchart *et al.* (1993), from P. Jepson and S. Schmitt's visit to Sumbawa from 10–23 September 1993 from B.R. Lees' visits to Moyo from 1992 to 1995; and from the Museum Zoologicum Bogoriense collection.

Pulau Sumbawa is an irregular shaped volcanic island 270 km long on its east-west axis and 90 km wide and covering about 14,750 km². Large bays (Teluk) in the central and eastern part of the island namely Teluk Saleh, Teluk Dompou, Teluk Bima and Teluk Waworada give the island its irregular shape. Teluk Saleh is the largest and divides the

island almost in half. Sumbawa contains several extinct volcanoes, the largest Gunung Tambora rising to 2821 m. The massive eruption of Tambora in 1815 produced 80 cubic kilometres of airborne ash which cooled the world enough to produce the year without a summer in 1816 (FAO 1981).

Collections and observations were made at fourteen main sites on Sumbawa namely: Desa Belo 8°52'00"S, 116°50'00"E, Desa Meraran 8°41'30"S, 116°51'00"E, Batu Hijau 9°00'S, 116°55'E, R.F2 (a meteorological station) 8°55'S, 117°00'E, Desa Merente 8°33'10"S, 117°01'15"E, Gunung Olet Sangenges 8°35'S, 117°07'E, Babar 8°55'S, 117°05'E, Batu Dulang 8°35'00"S, 117°17'20"E, Batu Tering 8°48'00"S, 117°22'00"E, around Sumbawa Besar 8°30'00"S 117°26'00"E, Teluk Santong 8°43'40"S, 117°53'30"E, Desa Daha (near Huu) 8°45'00"S, 118°26'00"E, Desa Waworada 8°42'30"S, 118°47'30"E, Desa Sangeang 8°18'00"S, 118°56'00"E and Sape 8°34'00"S, 119°00'00"E (Figure 2).

In the annotated list we summarise for each species its relative abundance (whether it is very common, common, moderately common, uncommon, scarce or rare), whether it feeds alone or in groups, status (whether it is a vagrant, visitor or resident), habitat preferences and breeding season.

Eight major habitat types were recognised on Sumbawa.

1. **Marine.** Includes coastal seas, straits between islands and gulfs.



Figure 1 Map of Nusa Tenggara showing position of Sumbawa Island.

2. **Mangal.** Small stands of mangal occur in many of the embayments. They consist mainly of *Rhizophora*, *Sonneratia* and *Bruguiera* in the seaward zone and *Avicennia*, *Lumnitzera* and *Excoecaria* to landward (Figure 3).
3. **Cultivated areas.** These include rice fields, coconut, cashew and banana plantations, village gardens with kapok, maize and other vegetables and in the highlands coffee plantations (Figure 4).
4. **Semi-evergreen rainforest, moist deciduous monsoon forest and gallery forest.** This forest is usually tall (canopy >30 m), is complex in structure and no doubt originally extended

over much of the volcanic-alluvial plain. Trees include, *Ficus*, *Terminalia*, *Alstonia*, *Celtis*, *Serianthes*, *Diospyros*, *Eugenia*, *Grewia*, *Schefflera*, *Myristica*, *Albizia*, *Mimusops*, *Garuga*, *Nauclea*, *Erythrina* and *Tamarindus*. Vines, rattans and palms are abundant and the understorey consists mostly of small trees, shrubs, bamboo, herbs, ferns and in some places *Lantana* (Figure 5).

Most of the lowland rainforest has been disturbed and cleared by shifting cultivation then allowed to regenerate. Historically it has also been locally devastated by volcanic eruptions and lava flows.



Figure 2 Map of Sumbawa, Moyo and Sangeang Islands showing main study sites.

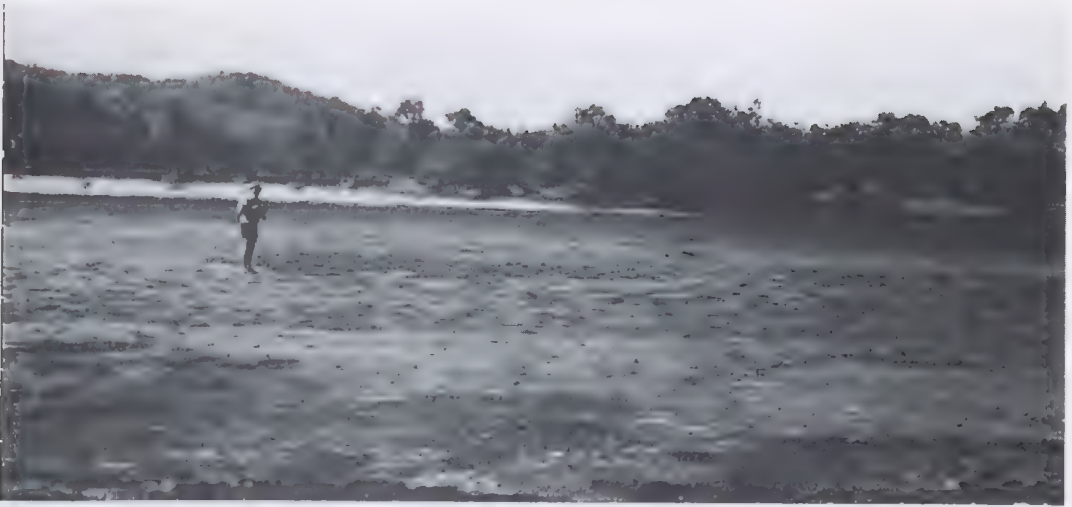


Figure 3 Mangal at Teluk Santong.

5. **Grassland.** Areas of rank grassland "alang alang", *Imperata cylindrica*, often with scattered trees and shrubs occur throughout the island (Figure 6).



Figure 4 Cultivated areas at Desa Daha, photographed by R. How.

6. **Woodland.** Open woodlands occur in drier parts of the island especially coastal flats on the eastern end. Trees include *Zizyphus*, *Acacia* and *Tamarindus* (Figure 7).

7. **Meraran wetland.** This is a large freshwater lake of about 860 ha with associated small swamps. The lake was largely carpeted with water hyacinth and water lilies and the swamps edged with stands of bulrush *Typha* and reeds *Pragmites* (Figure 8).

8. **Montane forest.** At about 700 m in altitude the lowland forest grades into montane rainforest. This change is well marked structurally and floristically and takes place through a broad ecotone of about 200–300 m in altitude. Structurally, the forest becomes lower (averaging about 20 m), the leaves smaller, and the tree trunks thinner stemmed and more heavily mossed. Many trees and shrubs occur that are not found at lower altitudes and epiphytes and ferns are abundant. At Batu Dulang this forest extended upwards to about 1200 m. On the higher peaks of Gunung Tambora above 1400 m the forest is largely dominated by *Casuarina junghuniana* with an understorey of herbaceous plants and ferns. Lower slopes of Tambora were once also clothed with pure stands of *Duabanga moluccana* highly prized for its timber, but most of this appears to have been cleared (Figure 9).

Pulau Moyo is an uplifted limestone island about 27 km long, 8–20 km wide, about 335 km² and with a maximum height of 200 m. It is situated 1.5 km off the northwest coast of Sumbawa near Sumbawa Besar at the mouth of Teluk Saleh. Three sites were visited on Moyo by the WAM-MZB expedition namely: Desa Sebotok 8°09'30"S, 117°37'15"E on



Figure 5 Semi-evergreen rainforest at Daha.



Figure 6 Grassland on eastern Sumbawa with Pulau Sangeang in background, photographed by R. How.



Figure 7 Open woodland near Sumbawa Besar.



Figure 8 Meraran wetland.



Figure 9 Montane forest at Merente.



Figure 10 Grassland at Tanjung Pasir.



Figure 11 Southern side of Pulau Sangeang, photographed by R. How.

northern end (between 6–9 November); Brang Kua 8°09'30"S, 117°36'45"E on eastern side (between 9–11 November); and Tanjung Pasir 8°23'15"S, 117°31'30"E on southern end (between 11–14 November). B.R. Lees visited areas on the west side of the island including the vicinity of Amanawana Bay 8°16'S, 117°30'E and Labuan Aji (Labuhanhaji) 8°13'S, 117°30'E.

Most of the southern half of the island consists of a rather extensive plateau undulating between 85 and 160 m. The northern half descends more gently to the sea, is more forested than the south, contains a more extensive drainage system, and has more land suitable for agriculture.

The major habitat types on Moyo Island are as follows:

1. **Mangal.** Many bays around the island contain small stands of mangroves. They consist mostly of a pioneer or seaward zone of *Sonneratia* and a landward zone of *Rhizophora* and *Bruguiera*.
2. **Semi-evergreen rainforest and moist deciduous monsoon forest.** This forest occurs over most of the northern half of the island on the central and southern slopes of the plateau and along southern creeks. The canopy has an average height of 20–25 m. Dominant trees include *Calophyllum*, *Cripteronis*, *Eugenia*, *Schoutenia*, *Grewia*, *Schleichera*, and *Protium*. Scattered trees of *Podocarpus* and *Dipterocarpus* occur mainly in the north.
3. **Grasslands.** Most of the central and southern part of the island consists of grassy plains with

emergent prickly trees and shrubs. (Figure 10).

4. **Cultivated areas and secondary regrowth.** This includes areas cleared for agriculture and depauperate scrubs with *Alstonia*, *Tamarindus* and *Lantana*.

Presumably the vegetation on Moyo would have been devastated by the eruption of Tambora in 1815.

Pulau Sangeang is a roughly circular volcanic island 15 km wide, 150 km² and with a central active volcano Gunung Api rising to 1949 m. It is situated 8 km off the northeast coast of Sumbawa and was visited between 21–23 October 1988 on the southwestern side at 8°13'30"S, 119°00'20"E. Gunung Api last erupted in 1986.

The narrow coastal fringe is vegetated mostly with low open woodland with a ground cover of rank grasses. Small thickets dominated mainly by *Ficus* spp. occur in some gullies but much of the vegetation has been disturbed by recent lava flows. Many derelict village gardens were overrun with castor oil plant. Large areas of 'alang alang' occur on the lower slopes of Gunung Api and patches of vine forest occur higher up and in deeper gullies. (Figure 11).

CLIMATE

Sumbawa, Moyo and Sangeang Islands have a tropical monsoon type climate, characterised by moderate stable temperatures and high relative humidity. The wet season (northwest monsoon)

begins in November, peaks in December–January and may continue until March. From May to September the winds are predominantly from the southeast (east monsoon) and are relatively dry. April and October are transitional. Mean daily temperatures range from 22–32° C, and average humidity is 85%. Mean annual rainfall ranges from 1000 mm in lowlands to 3000 mm in highlands. The eastern part of Sumbawa is considerably drier than the west.

ORNITHOLOGICAL HISTORY

Previous collections and additional data are available from:

1. J. Wivan van Lansberge 1880–1883, Governor General: Flores, Sumbawa, Alor and Timor (Junge 1954);
2. F. Guillemard, 1885, report on the collections of birds made during the voyage of the yacht 'Marchesa' (Bruce 1987);
3. W. Doherty 1887–1898, collector for Lord Rothschild on Sulawesi, Talaud 1887, 1891, 1896, Lombok, Sumbawa, Satonda, Bacan, Halmahera, Buru, Tanimbar, Obi and Kai (his hunters only) 1897–1898 (Junge 1954, Murphy 1932, Rothschild 1983);
4. J. Elbert 1909–1910, Sunda Expedition to Lombok, Sumbawa, Flores, Wetar, Muna, SE Sulawesi (Elbert 1911, Rensch 1926 and 1931, van Bemmelen and Voous 1951, Junge 1954 and Jany 1955);
5. B. Rensch's observations and collections from Lombok, Sumbawa and Flores (Rensch 1930, 1931);
6. G.A. Lincoln and others 1973, surveys of Lombok, Sumbawa and Komodo (Lincoln 1974, 1975);
7. FAO/UNDP Bogor 1981, survey Pulau Moyo and the Sanggar Peninsula (Gunung Tambora), a plan for conservation in northern Sumbawa;
8. The Birds of Wallacea (White and Bruce 1986);
9. D. Gibbs (1990) Wallacea, unpublished site guide for birdwatchers;
10. V. Mason (1990) Bali Bird Club Newsletter, No 1, unpublished;
11. K.D. Bishop (1992) New and interesting records of birds in Wallacea;
12. B.R. Lees' observations on Moyo from 1992–1995;
13. S.H.M. Butchart *et al.* 1993, Preliminary report of the Cambridge Flores/Sumbawa conservation project (unpublished report);
14. Collections in Museum Zoologicum Bogoriense (MZB).

ANNOTATED SPECIES LIST

Classification and nomenclature follows Andrew (1992) and White and Bruce (1986).

Hydrobatidae

Oceanites oceanicus Wilson's Storm-petrel

Sumbawa I. – One offshore an hour east of Sape on 20 August 1993. First recorded for Sumbawa by Bishop (1992).

Fregatidae

Fregata ariel Lesser Frigatebird

Sumbawa I. – Five between Sape and Komodo I. on 21 August 1993 also one probably this species offshore near Sumbawa Besar on 10 August 1993. Recorded by Gibbs (1990) between Sape and Komodo in December 1989 and Mason (1990) at Badas.

Moyo I. – Two just offshore between Sebotok and Brang Kua on 9 November 1988. These are the first records for the Sumbawa region.

Phalacrocoracidae

Phalacrocorax melanoleucus Little Pied Cormorant

Sumbawa I. – Flocks of 10 and 4 at a freshwater lake, Meraran on 13 May 1988, also one 5 km east of Alas on 9 August and another on 19 August 1993. The first records for Sumbawa.

Anhinga m. melanogaster Darter

Sumbawa I. – One calling from a freshwater lake at Meraran on 13 May 1988. Also one from Sumbawa Besar in MZB collection.

Sulidae

Sula leucogaster Brown Booby

Sumbawa I. – One just off Alas on 29 May 1988. The first record for Sumbawa.

Pelecanidae

Pelecanus conspicillatus Australian Pelican

Sumbawa I. – Uncommon vagrant from Australia. A flock of 300 recorded in western Sumbawa during May–December of 1978 (Somadikarta and Holmes 1979 and Escott and Holmes 1980).

Ardeidae

Ardea cinerea jouyi Grey Heron

Sumbawa I. – Two huge herons with white underparts, a black line through the eye and black flight feathers, were observed at a freshwater lake at Meraran on 13 May 1988. Rensch (1931) lists an immature female collected on Sumbawa in May.

Ardea sumatrana Great-billed Heron

Moyo I. – Single birds on coastal reefs at Tanjung Pasir on 13 and 14 November 1988, and two regularly observed in Amanwana Bay between 1992 and 1995. The first records for the Sumbawa region.

Ardea purpurea Purple Heron

Sumbawa I. – Two at a freshwater lake at Meraran on 13 May 1988 and two at Lake Taliwang, east of Maluku on 9 August 1993.

Ardea novaehollandiae White-faced Heron

Sumbawa I. – Moderately common, in ones, twos and small groups (up to 8) occasionally larger aggregations (up to 50). Recorded at Meraran, Lake Taliwang, Babar, Selah Legium, Belo, Dompou and Dahu. Rice fields, freshwater lakes and creeks.

Moyo I. – One on coast at Brang Kua on 10 November 1988.

Egretta alba Great Egret

Sumbawa I. – One at a swamp near Empang on 20 May and three on a mudflat near Bima on 19 October 1988. The first records for Sumbawa.

Egretta garzetta Little Egret

Sumbawa I. – Seven on mudflats at Sape on 21 August 1993. The first record for Sumbawa.

Egretta sacra Reef Egret

Sumbawa I. – Three near Maluku on 9 August and one at Sape on 21 August 1993. All grey phase.

Moyo I. – One on SW coast and two on reefs at Tanjung Pasir in November 1988. Also groups of four to five at Amanwana Bay from 1992–1995. Both white phase and dark phase birds recorded.

Bubulcus ibis Cattle Egret

Sumbawa I. – Locally common but generally uncommon. One in rice field at Batu Tering on 8 May 1988 and at least 1000 at Lake Taliwang on 9 August 1993.

Ardeola speciosa Javan Pond Heron

Sumbawa I. – Common in lowland wetlands. Small groups and loose flocks (up to 300). Recorded at Meraran, Lake Taliwang, Belo, Dompou, Waworada, Dahu, Sape and Sumbawa Besar. Rice fields, swamps, lakes, along rivers and mudflats.

Moyo I. – Moderately common. Small groups (up to 8). Recorded at Sebotok and Brang Kua. Mainly rice fields and mangal.

Butorides striatus Striated Heron

Sumbawa I. – Moderately common in mangal at Teluk Santong in May and in dense creekside vegetation at Dahu in October 1988, also in lowland riverine forest at Selah Legium in August 1993.

Moyo I. – Common to moderately common. Recorded at Sebotok, Brang Kua and Tanjung Pasir. Mangal, tidal flats and beaches. Nest with 2 eggs (one chipping) 9 m up in a *Sonneratia alba* on seaward edge of mangal at Sebotok on 7 November 1988.

Ixobrychus sinensis Yellow Bittern

Sumbawa I. – Moderately common at a large freshwater lake at Meraran in May 1988. Mainly in Typha, lilies and water hyacinth. Nest with one nestling found in Typha on 13 May. This is the first record for

Sumbawa and the first breeding record for Nusa Tenggara. Previously thought to be only a migrant to Wallacea, however, small breeding populations have been found in areas with a large influx of migrants e.g. Sri Lanka, the Philippines and Java (Hancock and Elliott 1978).

Ciconiidae

Ciconia e. episcopus Woolly-necked Stork

Sumbawa I. – Moderately common in ones, twos and groups (up to 30). Recorded at Belo, Sekongkang (8°59'S, 116°45'E), Selah Legium and near Sumbawa Besar. Mainly ricefields. Two specimens from Dompou in MZB collection.

Moyo I. – Scarce. Two at Brang Kua on 11 November, two on a reef flat at Tanjung Pasir on 14 November 1988 and two observed regularly between Labuan Aji and waterfalls from 1992–1995.

Leptoptilos javanicus Lesser Adjutant

Moyo I. – Two at Brang Kua on 10 November 1988. The first record east of Bali.

Accipitridae

Pandion haliaetus Osprey

Moyo I. – Scarce. Only recorded at Amanwana Bay and Tanjung Pasir.

Pernis ptilorhynchus Oriental Honey-buzzard

Sumbawa I. Scarce. One at Babar, Selah Legium on 8 August and a pair at Gunung Olet Sangenges on 16 August 1993. These are the first records for Sumbawa and the birds probably belong to one of the Sundaic races *P. p. torquatus* or *P. p. ptilorhynchus*.

Elanus caeruleus Black-winged Kite

Sumbawa I. – Scarce. Recorded by Gibbs (1990) at Taliwang in December 1989 and one near Lake Taliwang on 9 August 1993. The first records for Sumbawa.

Milvus migrans affinis Black Kite

Sumbawa I. – Three edge of lake at Meraran on 22 May and one over roads and fires on 13 May 1988. The first records for Sumbawa.

Haliastur indus intermedius Brahminy Kite

Sumbawa I. – Common. Ones, twos and groups (up to 24). Recorded at Alas, Meraran, Selah Legium, Maluku, Taliwang, Sumbawa Besar, Teluk Santong, Dahu and near Dompou. Mainly coasts, swamps, riverine vegetation and moist deciduous monsoon forest. Also attracted to fires. Recorded up to 1200 m at Gunung Olet Sangenges. A male from Dompou in MZB collection.

Moyo I. – One in mangal and coconut plantation at Sebotok, two observations of single birds at Tanjung Pasir and two at Amanwana.

Haliaeetus leucogaster White-bellied Sea Eagle

Sumbawa I. – Uncommon. One near Alas on 7 May; one near Sumbawa Besar on 23 May 1988; one at Maluku on 9 August 1993; four east of Sape on 21 August 1993;

and one inland at 1250 m at Gunung Olet Sangenges on 18 August 1993. Also one on islet between Sumbawa and Lombok on 29 May 1988.

Moyo I. – One at Tanjung Pasir on 12 November 1988 and a pair breeding each year at Amanwana from 1992–1995.

Circus gallicus Short-toed Eagle

Sumbawa I. – One record of two birds at Babar, Selah Legium on 5 August 1993.

Accipiter fasciatus wallacii Brown Goshawk

Sumbawa I. – Uncommon to moderately common. Ones and twos recorded at Belo, Babar (Selah Legium), Gunung Olet Sangenges, Dahu and Sumbawa Besar. Rainforest and riverine forest. A female from Sumbawa Besar in MZB collection.

Moyo I. – Two in rainforest at Brang Kua on 10 November and a pair building a nest 13 m up in *Erythrina* in vine forest at Tanjung Pasir in November 1988. Also recorded at Amanwana. The stomach of a male collected at Brang Kua contained a lizard *Sphenomorphus*.

Sangeang I. – One hunting over prickly *Acacia-Zizyphus* scrub on 21 October 1988.

Accipiter novaehollandiae sylvestris Grey Goshawk

Sumbawa I. – Uncommon. Recorded during July–August 1993 at all three sites in Selah Legium complex and at Gunung Olet Sangenges up to 900 m. Mainly in rainforest but also moist deciduous monsoon forest. Two specimens from Sumbawa Besar in MZB collection.

Moyo I. – One in coconut palms at Sebotok on 7 November 1988. Also observed in several locations around the island by B. Lees between 1992 and 1995.

Accipiter gularis Japanese Sparrow-hawk

Sumbawa I. – One at Batu Hijau on 27 July and two on 28 July 1993. This is a common Palaearctic winter visitor to South-East Asia but there are few records for the Lesser Sundas and these are the first for Sumbawa.

Hieraaetus fasciatus Bonelli's Eagle

Sumbawa I. – Rare. Two just east of Maluku on 9 August 1993.

Hieraaetus kienerii Rufous-bellied Eagle

Sumbawa I. – Rare. Three records at Batu Hijau and one at Gunung Olet Sangenges in July–August 1993. The first records for Sumbawa and this species is listed by White and Bruce (1986) as scarce and local in Wallacea.

Spizaetus cirrhatus floris Changeable Hawk-eagle

Sumbawa I. – Rare. One at Gunung Olet Sangenges on 15 August 1993 and a male from Batu Dulang in MZB collection. This subspecies is restricted to Flores, Sumbawa and Paloe, and is isolated from the nearest breeding birds in South-East Asia.

Falconidae

Falco moluccensis microbalia Spotted Kestrel

Sumbawa I. – Moderately common. Ones and twos.

Recorded at Meraran, Belo, Babar, Selah Legium, Maluku, Batu Tering, the footslopes of Gunung Olet Sangenges, Sumbawa Besar, Dompou, Waworada and Batu Dulang. Forests, woodlands, near large bat caves, lowland open country and around villages. Pair entering a hollow 25 m up in huge tree in rainforest at Batu Dulang (alt. 800 m) on 4 November 1988.

A male from Dompou in MZB collection.

Moyo I. – Scarce, Ones and twos at Amanwana, Labuan Aji, Sebotok, Brang Kua and Tanjung Pasir. Coconut plantations, rice fields and over burnt areas.

Falco cenchroides Australian Kestrel

Sumbawa I. – One at Sekongkong, western Sumbawa (8°59'S, 116°45'E) on 1 August 1993. The first record for Sumbawa.

Falco longipennis Australian Hobby

Sumbawa I. – Scarce or uncommon. Six sightings, mostly of single birds at Selah Legium, Batu Tering, near Dompou and at Batu Dulang. Over villages and rice fields.

Moyo I. – Two observations of a single bird hunting over low prickly *Zizyphus* and coastal cliffs at Tanjung Pasir.

Anatidae

Dendrocygna javanica Lesser Whistling Duck

Sumbawa I. – Ten trapped by a fisherman on freshwater lake at Meraran on 12 May 1988.

Anas gibberifrons Grey Teal

Moyo I. – Several observations of two birds on brackish coastal pools at Tanjung Pasir.

Megapodidae

Megapodius r. reinwardt Orange-footed Scrubfowl

Sumbawa I. – Scarce or rare. Only recorded at Belo and at Batu Hijau and RF2, Selah Legium. Ones and twos in lowland rainforest and prickly vine forest.

Moyo I. – Moderately common. Recorded at Brang Kua and Tanjung Pasir. Rainforest, creekside forest and prickly coastal scrub. Birds were active on mounds in November.

Sangeang I. – Scratchings probably made by this species were found along a creek with dense vine forest.

Phasianidae

Gallus varius Green Junglefowl

Sumbawa I. – Moderately common to very common and widespread. Recorded at Merante, three sites in Selah Legium, Gunung Olet Sangenges, Belo, Batu Tering, Desa Sangeang, Waworada, Dahu, near Dompou, Batu Dulang and near Sumbawa Besar. Sea level to 1500 m. Mossy forest, rainforest, vine forest, bamboo thickets and open woodland. More often heard than seen. A downy chick collected at Waworada on 27 October 1988.

Moyo I. – Locally moderately common but generally scarce. Calling at Brang Kua and Tanjung Pasir in 1988, also recorded in a number of localities by B. Lees between 1992 and 1995.

Sangeang I. – Scarce. Thickets and scrubs.

Turnicidae

Turnix maculosa floresiana Red-backed Button-quail

Sumbawa I. – Scarce. Seven at Desa Sangeang on 20 October 1988. A male from Sumbawa Besar in MZB collection.

Sangeang I. – A small quail probably this species was flushed from a grassy flat with prickly *Acacia* on 21 October.

Turnix suscitator powelli Barred Button-quail

Sumbawa I. – A female from Sumbawa Besar in MZB collection.

Moyo I. – One probably this species flushed from strand zone on beach at Sebotok on 8 November and another from grassland at Brang Kua on 10 November 1988.

Sangeang I. – An adult and chick trapped in grassland.

Rallidae

Rallina fasciata Red-legged Crake

Sumbawa I. – Two edge of freshwater lake at Meraran on 13 May 1988, one in wet grass on the edge of a flooded rice field at Belo on 17 May 1988 and one mist-netted in lower montane forest at c. 550 m at Gunung Olet Sangenges on 16 August 1993. The first records for Sumbawa.

Porzana cinerea White-browed Crake

Sumbawa I. – Ones and twos at Meraran in May 1988. Freshwater lake with lilies, bulrushes and water hyacinth.

Amaurornis phoenicurus leucomelanus White-breasted Waterhen

Sumbawa I. – Uncommon to moderately common. Recorded Meraran, Lake Taliwang, Belo, Babar, Selah Legium, Gunung Olet Sangenges, Waworada and near Domp. Rice fields, swamps, edges of rivers and creeks.

Porphyrio porphyrio Purple Swamphen

Sumbawa I. – Two at edge of a freshwater lake at Meraran on 12 and 13 May 1988. Both had greenish-grey backs. The first record for Sumbawa.

Gallinula tenebrosa Dusky Moorhen

Sumbawa I. – One, probably this species observed on a freshwater lake at Meraran on 13 May 1988.

Gallinula chloropus Common Moorhen

Sumbawa I. – Two on freshwater lake at Meraran on 12 and 13 May 1988. Both were adults with black upperparts, white flanks and red base to bill. White and Bruce (1986) list a juvenile collected in May.

Jacaniidae

Irediparra gallinacea Comb-crested Jacana

Sumbawa I. – Up to six at freshwater lake, Meraran in May 1988. Feeding among lilies and water hyacinth.

Charadriidae

Pluvialis squatarola Grey Plover

Sumbawa I. – One on coastal flats near Bima on 19 October 1988 and one adult on mudflats at Sape on 21 August 1993. First records for Sumbawa.

Moyo I. – Ones, twos and once a loose group of 8 at Tanjung Pasir in November 1988.

Pluvialis fulva Pacific Golden Plover

Moyo I. – Two on tidal flats at Desa Sebotok on 6 November 1988.

Charadrius peronii Malaysian Plover

Sumbawa I. – Uncommon along the northern coast. Six on a muddy beach near Maluku on 9 August 1993, three near Sumbawa Besar on 11 August and two on mudflats at Sape on 21 August 1993; also two birds probably *C. peronii* observed twice at edge of mangal, Teluk Santong in May 1988.

Charadrius leschenaultii Greater Sand-plover

Sumbawa I. – Scarce or uncommon. One 5 km east of Alas on 9 August 1993, four probably this species near same place on 11 August, and at least six on mudflats at Sape on 21 August 1993. Also recorded by Gibbs (1990) at Taliwang in December 1989. The first records for Sumbawa.

Moyo I. – Two possibly *C. leschenaultii* on mud flats at Desa Sebotok on 6 November 1988.

Scolopacidae

Numenius phaeopus Whimbrel

Sumbawa I. – One on mudflats near Bima on 19 October 1988, and one on a beach 5 km east of Sumbawa Besar on 10 August 1993. A passage migrant and winter visitor to Wallacea.

Moyo I. – Moderately common in November 1988. Mudflats, exposed reefs and beaches.

Numenius madagascariensis Far-Eastern Curlew

Sumbawa I. – Two 5 km east of Alas on 9 August 1993. The first records for Sumbawa.

Limosa lapponica Bar-tailed Godwit

Sumbawa I. – Three on mudflats near Alas on 28 May, and one on a beach near Waworada on 27 October 1988. The first records for Sumbawa. A passage migrant and winter visitor to Wallacea.

Moyo I. – One on a tidal flat at Sebotok on 6 November 1988.

Tringa totanus Common Redshank

Sumba Is. – three on mudflats at Sape on 21 August, 1993.

Moyo I. – Two on beach at Tanjung Pasir on 12 November 1988. The first records for the Sumbawa region.

Xenus cinereus Terek Sandpiper

Sumbawa I. – Two on mudflats at Sape on 21 August 1993. The first record for Sumbawa.

Heteroscelus brevipes Grey-tailed Tattler

Sumbawa I. – Moderately common. Recorded at Teluk Santong, near Alas, Empang and near Bima. Coastal mudflats. A passage migrant and winter visitor. The first records for Sumbawa.

Moyo I. – Moderately common. Tidal flats and beaches.

Tringa hypoleucos Common Sandpiper

Sumbawa I. – Moderately common. Regularly observed on beaches, mudflats and rocky shores along the northern coast.

Moyo I. – Moderately common in November 1988. Recorded at Sebotok, Brang Kua and Tanjung Pasir. Beaches, mudflats and mangal.

Sangeang I. – One on coastal rocks and one on a beach.

Recurvirostridae*Himantopus leucocephalus* White-headed Stilt

Sumbawa I. – Two in rice fields near Sumbawa Besar on 8 May 1988.

Phalaropodidae*Phalaropus lobatus* Red-necked Phalarope

Sumbawa I. – Forty-nine offshore east of Sape on 21 August 1993. A passage migrant and winter visitor to Wallacea.

Moyo I. – Four feeding on calm sea in strait between Tanjung Pasir (Moyo I.) and Sumbawa I. on 14 November 1988.

Burhinidae*Esacus magnirostris* Beach Stone Curlew

Moyo I. – One on reef at Tanjung Pasir on 14 November 1988, also recorded in ones and twos at Amanwana Bay and along the east coast by B. Lees between 1992 and 1995.

Laridae*Sterna anaethetus* Bridled Tern

Sumbawa I. – A total of 149 birds offshore east of Sape on 21 August 1993.

Sterna albifrons sinensis Little Tern

Sumbawa I. – Flocks of 100, 50, 20, 10, 30 and 100 were recorded flying north between Lombok and Sumbawa on 18 October 1988. This region is part of the migration flyway between South East Asia and its winter quarters in northern Australia. Small numbers also breed in the eastern Lesser Sundas.

Sterna bergii Great Crested Tern

Sumbawa I. – Scarce. Two in the port of Alas in May 1988, 6 at sea between Sumbawa and Lombok in October 1988 and twenty offshore east of Sape on 21 August 1993. Also reported by Mason (1989).

Moyo I. – Scarce. Four feeding along shoreline near Tanjung Pasir on 13 November 1988 and one at sea between Moyo and Sumbawa Is on 14 November 1988. These are the first records for the Sumbawa region.

Sterna bengalensis Lesser Crested Tern

Sumbawa I. – One just east of Sape on 21 August 1993. The first record for Sumbawa.

Cygis alba White Tern

Sumbawa I. Two offshore east of Sape on 21 August 1993. The first record for Sumbawa and for Wallacea (White and Bruce 1986).

Columbidae*Treron floris* Flores Green Pigeon

Sumbawa I. – One in lowland semi-evergreen forest at 550 m at Batu Hijau, Selah Legium on 30 July 1993.

Treron vernans Pink-necked Green Pigeon

Sumbawa I. – Two in low prickly scrub on a dry hill at Desa Sangeang on 20 October 1988; moderately common in rainforest at Waworada, small flocks flying high and fast over forest. Breeding March–May (White and Bruce 1986).

Moyo I. – Two feeding on fruits of *Eugenia cummini* and another two in *Ficus* and *Terminalia* at Sebotok in November 1988.

Sangeang I. Moderately common. Ones, twos and small flocks (up to 50). Prickly *Zizyphus* and *Acacia* also creekside vegetation with fruiting trees especially *Ficus*.

Previously recorded only from Lombok I. and Sumbawa I.

Ptilinopus cinctus albocinctus Black-backed Fruit Dove

Sumbawa I. – Locally moderately common to common but generally scarce. Recorded in montane forest at 1150 m at Batu Dulang in November 1988, at two sites in lowland semi-evergreen rainforest at Selah Legium in August 1993 and at Gunung Olet Sangenges in August 1993. At the latter common in lower montane forest from 800 m to 1000 m and abundant in montane forest from 1000 to 1500 m. Mainly pairs and small groups. Call a loud 'how-wow' or 'coo-woop'.

Ptilinopus melanospila Black-naped Fruit Dove

Sumbawa I. – Uncommon. Two in canopy of rainforest at Waworada in October 1988, also recorded at Gunung Olet Sangenges and at three sites at Selah Legium during July–August 1993. Mainly moist deciduous monsoon forest, semi-evergreen forest, lowland forest and lower montane forest, from 50 m to 700 m.

Moyo I. – Two in a coastal thicket with *Tamarindus*, *Sesbania* and *Eugenia*.

Sangeang I. – Two feeding in canopy of huge *Ficus* on 23 October 1988.

Ducula aenea polia Green Imperial Pigeon

Sumbawa I. – Uncommon to very common, in pairs and small groups. Recorded at Sumbawa Besar,

Merente, Belo, Gunung Olet Sangenges, three sites in Selah Legium and Dahu. Recorded up to 850 m. Most common in lowland semi-evergreen rainforest, less frequent in moist deciduous monsoon forest below 100 m and in lower montane forest above 600 m.

Moyo I. – Common. Ones, twos and flocks (up to 50). Recorded at Amanwana, Sebotok and Brang Kua. Rainforest especially areas with fruiting trees including *Eugenia cummini* and *Ficus*. Also observed flying between Tanjung Pasir and Sumbawa I.

Ducula lacernulata Dark-backed Imperial Pigeon

Sumbawa I. – Common above 850 m in montane forest at Gunung Olet Sangenges during August 1993. Recorded up to 1700 m. Mostly in upper montane ridge-top forest. A pair carrying nesting material at 1460 m on 15 August. The first records for Sumbawa.

Ducula bicolor Pied Imperial Pigeon

Moyo I. – Rare. Several flocks observed by R. Lees at Labuan Aji between 1992 and 1995.

Columba vitiensis Metallic Pigeon

Sumbawa I. – Scarce or rare. Five records of single birds during August 1993. Recorded in lowland semi-evergreen forest at Batu Hijau, in moist deciduous monsoon forest at Babar and in upper montane forest at 1250 m at Gunung Olet Sangenges. Presumably rare, but widespread and inhabiting a variety of forest types.

Macropygia emiliana Ruddy Cuckoo-dove

Sumbawa I. – Status uncertain. Rare in lowland semi-evergreen forest at the two sites at Selah Legium and in lower montane forest below 1000 m at Gunung Olet Sangenges; but common in upper montane forest (up to 1600 m) at Gunung Olet Sangenges.

Sangeang I. – Four in a *Ficus* thicket along a gully on 23 October.

Macropygia ruficeps orientalis Little Cuckoo Dove

Sumbawa I. – One probably this species in mossy rainforest at 1150 m near Batu Dulang in November 1988. Breeding recorded in May (White and Bruce 1986). A male from Batu Dulang in MZB collection.

Moyo I. – One in vine forest at Tanjung Pasir on 14 November 1988.

Streptopelia bitorquata Island Collared Dove

Sumbawa I. – Common in mangal at Teluk Santong. Listed as breeding in April–May (White and Bruce 1986).

Moyo I. – Scarce. Only recorded at Desa Sebotok. Mangal.

Sangeang I. – Three on beach on 22 October 1988.

Streptopelia chinensis tigrina Spotted Dove

Sumbawa I. – Common and widespread. Recorded at Alas, near Sumbawa Besar, Merente, Belo, Gunung Olet Sangenges, Maluk, Babar, Teluk Santong, Batu Tering, Sangeang and Dahu. Mainly in and around cultivation but also open coastal woodland, open *Acacia* scrub and riverine vegetation. From sea level to c. 800 m. Listed as breeding from March to May (White and Bruce 1986).

Moyo I. – Moderately common. Recorded at Labuan Aji, Desa Sebotok, Brang Kua and Tanjung Pasir. Creekside vegetation, edges of rainforest, burnt areas and prickly coastal scrub.

Sangeang I. – Common. Groups of up to 100 drinking from seepages on beaches. Also open forest and woodland.

Geopelia striata maugei Timor Zebra Dove

Sumbawa I. – Common. Recorded at Belo, Babar, Teluk Santong, Waworada, Maluk, Sura I., and Dahu. Edges of forest and mangal, along creeks also rice fields, gardens, scrub and road verges below 100 m. Breeding April–July (White and Bruce 1986).

Moyo I. – Moderately common. Recorded at Labuan Aji, Sebotok and Brang Kua. Edges of mangal, gardens and open woodland.

Sangeang I. – Common. Ones, twos and groups of up to 50 drinking at fresh water seepages on beach. Also coastal scrubs and woodlands.

Chalcophaps indica indica Green-winged Pigeon

Sumbawa I. – Scarce or uncommon. Recorded at Batu Tering at three sites at Selah Legium and at Gunung Olet Sangenges. Creekside forest, bamboo thickets, lowland semi-evergreen and moist deciduous monsoon forest, and lower montane forest (up to 850 m). Rare in upper montane forest.

Moyo I. – Scarce. Only recorded at Sebotok. Coastal vine thickets and mangal.

Sangeang I. – One in creekside forest.

Caloenas nicobarica Nicobar Pigeon

Sumbawa I. – Scarce. One flushed from edge of open forest at Belo on 17 May 1988 and three records of possibly the same individual in semi-evergreen lower montane forest at 450 m at Batu Hijau, Selah Legium in August 1993. Also a female from Taliwang in MZB collection.

Moyo I. – Scarce. Several flocks of 8–10 observed by B. Lees in dense forest near waterfalls between 1992 and 1995.

Psittacidae

Trichoglossus haematodus forsteni Rainbow Lorikeet

Sumbawa I. – Uncommon to moderately common in small flocks (up to 8). Recorded at Alas, Sumbawa Besar, Merente, Belo, RF2, Babar, Waworada and Batu Dulang. Coastal lowlands, moist deciduous monsoon forest and rainforest to 1150 m. Nomad attracted to flowering trees.

Cacatua sulphurea parvula Yellow-crested Cockatoo

Sumbawa I. – Rare. One in semi-evergreen rainforest at Merente on 11 May 1988; a pair in tall riverine forest dominated by the tree *Duabanga moluccensis* at RF2, Selah Legium on 5 August 1993 and one at same place the following day. This parrot appears to be close to extinction on Sumbawa.

Moyo I. – Moderately common. Small groups (up to 5) recorded at Brang Kua and Tanjung Pasir. Rainforest and gardens.

Geoffroyus geoffroyi floresianus Red-cheeked Parrot

Sumbawa I. – Locally common, e.g. at Gunung Olet Sangenges, at three sites at Selah Legium and at Waworada and Dahu, elsewhere scarce. Lowland semi-evergreen and moist deciduous monsoon forest below 550 m (uncommon above 550 m to 700 m), also woodland and sometimes village gardens.

Cuculidae*Cuculus saturatus* Oriental Cuckoo

Sumbawa I. – Rare. One in bamboo thicket near Dompou on 1 November 1988; listed as rare in moist deciduous monsoon and lowland semi-evergreen forest at RF2 and Babar, Selah Legium in August 1993; and rare in lowland semi-evergreen and montane forest (up to 1400 m) at Gunung Olet Sangenges in August 1993. Both migrant *C. s. saturatus* and resident *C. s. lepidus* are recorded for this island.

Moyo I. – One in prickly scrub at Tanjung Pasir on 11 November 1988.

Cuculus sepulcralis Rusty-breasted Cuckoo

Sumbawa I. – Recorded as rare in lowland semi-evergreen forest below 550 m, but common in montane forest up to 1500 m at Gunung Olet Sangenges in August 1993.

Sangeang I. – One in creekside forest on 23 October 1988.

Chrysococcyx lucidus Shining Bronze-cuckoo

Sumbawa I. – Rare. Only recorded at three sites at Selah Legium and at Gunung Olet Sangenges in August 1993. Moist deciduous monsoon forest and lowland semi-evergreen forest below 550 m.

Eudynamis scolopacea Asian Koel

Sumbawa I. – Scarce. Single birds at Waworada in October 1988 and in scrub at Babar, Selah Legium in August 1993.

Moyo I. – Moderately common. Ones and twos. Recorded at Sebotok, Brang Kua and Tanjung Pasir. Mangal, forest with fruiting trees and open prickly *Zizyphus*.

Centropus bengalensis javanensis Lesser Coucal

Sumbawa I. – Locally moderately common. Recorded at Batu Tering, Meraran, Belo, two sites at Selah Legium, Batu Hijau, Babar, Sangeang, Waworada, Dahu, Batu Dulang and Dompou. Tall grass, gardens, *Lantana* thickets, lowland semi-evergreen forest, scrub and edges of rainforest. From coasts to 1150 m.

Moyo I. – Uncommon. Ones and twos at Labuan Aji, Brang Kua and Tanjung Pasir. Hedge rows, *Lantana* and prickly *Zizyphus*.

Tytonidae*Tyto alba* Barn Owl

Sumbawa I. – One entangled in string in a coconut palm at Sumbawa Besar in November 1988.

One specimen (spirit), length 33 cm, weight 294 g.

Moyo I. – One at Tanjung Pasir in 1992, also heard at Amanwana between 1992 and 1995.

Strigidae*Otus magicus albiventris* Moluccan Scops Owl

Sumbawa I. – One collected from open forest at Waworada and two netted in gardens with coconut palms, bamboo and kapok at Dahu in October 1988.

Otus silvicola Wallace's Scops Owl

Sumbawa I. – Status uncertain. A total of seven birds heard calling in lowland semi-evergreen rainforest at 500–550 m at Batu Hijau, Selah Legium and at 450 m at Gunung Olet Sangenges, and one in upper montane forest at 1350 m at the latter site. Also a male from Dompou in MZB collection.

Caprimulgidae*Caprimulgus macrurus* Large-tailed Nightjar

Sumbawa I. – Four edge of forest at Batu Tering in May 1988, one calling from a clearing in rainforest at Batu Dulang (1150 m) in November 1988 and two sightings of single birds in a forest clearing at Batu Hijau, Selah Legium in July and August 1993.

Caprimulgus affinis Savanna Nightjar

Sumbawa I. – Uncommon. Recorded at Waworada and near Dompou. Grassland on stony hills, open woodland, bare flats and edges of roads.

Moyo I. – One in open prickly woodland near Tanjung Pasir on 12 November 1988.

Sangeang I. – One on open grassy flat on 22 October 1988. Call 'skeetch' or 'tweetch'.

Apodidae*Aerodramus fuciphagus* Edible-nest Swiftlet

Sumbawa I. – Locally common but generally uncommon. Five collected from an old Japanese tunnel at 800 m near Batu Dulang in November 1988. Common at three sites at Selah Legium and at Gunung Olet Sangenges (mainly below 1000 m). About 50,000 at Lake Taliwang on 9 August 1993.

Collocalia esculenta Glossy Swiftlet

Sumbawa I. – Common to very common. From sea level to 1250 m. Recorded at Alas, Merente, Belo, Selah Legium, Maluk, Gunung Olet Sangenges, Sumbawa Besar, Batu Tering, Dahu and Batu Dulang. Breeding at Belo in May 1988.

Sangeang I. – Common. Seven collected from a small cave.

Hirundapus caudacutus White-throated Needletail

Moyo I. – Two dashing low over the coast during a thunderstorm at Tanjung Pasir on 13 November 1988. The first record for the Sumbawa region.

Cypsiurus balasiensis Asian Palm Swift

Sumbawa I. – Four, probably this species, were flushed from the dead skirt of a coconut palm at

Sumbawa Besar on 5 November 1988. White and Bruce (1986) list unconfirmed reports from Komodo, Rinca and Flores I.

Moyo I. – Two flushed twice from frons of a coconut palm at Sebotok on 8 November 1988.

Alcedinidae

Alcedo atthis floresiana Common Kingfisher

Sumbawa I. – Uncommon. Recorded in riverine forest at RF2 and Babar, Selah Legium in August 1993. Also a male from Sumbawa Besar in MZB collection.

Alcedo meninting Blue-eared Kingfisher

Sumbawa I. – One collected at Batu Tering on 26 May 1988. The first record for Sumbawa.

Alcedo coerulescens Small Blue Kingfisher

Sumbawa I. – Locally moderately common e.g. in mangal at Teluk Santong, elsewhere scarce. Also recorded at Meraran at edge of swamp and at Empang.

Ceyx erithacus Oriental Dwarf Kingfisher

Sumbawa I. – Uncommon in riverine forest at three sites at Selah Legium (up to 550 m), and a single record at 650 m at Gunung Olet Sangenges in August 1993.

Halycon capensis floresiana Stork-billed Kingfisher

Sumbawa I. – Scarce or rare. One in mangal at Teluk Santong on 23 May 1988, also recorded in riverine forest at three sites at Selah Legium and at Gunung Olet Sangenges in August 1993. Most records below 550 m one at 870 m.

Halcyon sancta Sacred Kingfisher

Sumbawa I. – Common. Ones and twos. Recorded at Sumbawa Besar, Meraran, Belo, Teluk Santong, Batu Tering and Dahu in 1988 and along the coast between Maluku and Sumbawa Besar and at Sape in August 1993. Mangal, village gardens, open woodland and edges of forest. Mainly a winter visitor from Australia.

Moyo I. – Scarce. One in mangal at Sebotok on 7 November 1988, also recorded at Tanjung Pasir and Amanwana between 1992 and 1995.

Sangeang I. – Scarce. Single birds in prickly *Zizyphus* scrub on 21 and 22 October 1988.

Halcyon chloris chloris Collared Kingfisher

Sumbawa I. – Common. Ones and twos. Recorded at Teluk Santong, Bima, Sangeang and Waworada in May 1988 and along the coast from Maluku to Sape in August 1993. Mainly mangal and village gardens. Observed feeding on fiddler crabs at Teluk Santong.

Moyo I. – Uncommon. Ones and twos. Recorded at Sebotok and Tanjung Pasir. Mangal and coastal scrub also groves of *Tamarindus*.

Sangeang I. – Uncommon. Ones and twos in open woodland near coast.

Caridonax fulgidus White-rumped Kingfisher

Sumbawa I. – Uncommon but locally moderately common. A female collected from rainforest at Batu Dulang on 3 November 1988, also recorded from 50–

1460 m at Gunung Olet Sangenges and at three sites at Selah Legium in August 1993. Most frequent in primary semi-evergreen forest (particularly in lower montane forest at Gunung Olet Sangenges), but also recorded in moist deciduous monsoon forest and forest edges. A female from Bau Dulang in MZB collection.

Meropidae

Merops ornatus Rainbow Bee-eater

Sumbawa I. – Common in pairs and flocks (up to 300). Recorded at Alas Batu Tering, Merente, near Taliwang, Belo, Batu Hijau, Maluku, Gunung Olet Sangenges, near Sumbawa Besar, Batu Dulang, Teluk Santong, Sangeang, Waworada and near Sape. Probably mostly winter visitors from Australia, records in May, July–August and October–November. A flock of 100 flying north over Merente on 11 May 1988 and a flock of 300 roosting in mangal at Teluk Santong on 21 May 1988. Some breeding may also occur in the region. A freshly dug but empty nest burrow was found on an open grassy flat at Sangeang on 20 October 1988. Breeding occurs in north Western Australia in October–February.

Moyo I. – Common along edge of mangal at Sebotok, also recorded at Tanjung Pasir.

Sangeang I. – Scarce. Two on 22 October and 4 on 23 October 1988.

Merops philippinus Blue-tailed Bee-eater

Sumbawa I. – Scarce. Recorded at Alas and Meraran in 1988, and two 5 km east of Sumbawa Besar on 10 August 1993.

Moyo I. – Scarce. Migratory flocks observed by R. Lees at Labuan Aji, mainly August–October.

Coraciidae

Eurystomus orientalis Common Dollarbird

Sumbawa I. – Status uncertain. Two in riverine forest at Dahu on 31 October 1988, one near Dompur in November 1988 also recorded in open areas with scattered trees at three sites at Selah Legium in July–August 1993.

Moyo I. – A female collected from tall *Sonneratia* mangal at Sebotok on 7 November 1988. Listed by R. Lees as often seen on west side of island.

Picidae

Dendrocopos moluccensis Brown-capped Woodpecker

Sumbawa I. – Locally moderately common but generally scarce. Recorded at Batu Dulang in November 1988 and at three sites at Selah Legium and at Gunung Olet Sangenges in July–August 1993. Mainly semi-evergreen forest also lower montane forest up to 850 m, scarce or rare in lowland moist deciduous monsoon and upper montane forest.

Sangeang I. – One in open woodland on 23 October 1988.

Pittidae

Pitta elegans concinna Elegant Pitta

Sumbawa I. – Locally moderately common to

common. Recorded at Merente, near Alas, Belo, Batu Dulang, at three sites at Selah Legium and at Gunung Olet Sangenges. Recorded from 30–1350 m. Common in logged forest, frequent in primary semi-evergreen and moist deciduous monsoon forest, uncommon in upper montane forest. Three mist-netted birds had brood patches on 2, 13 and 14 August.

Alaudidae

Mirafra javanica Singing Bushlark

Sumbawa I. – Scarce. One on a bare rice field at Belo on 15 and 16 May and one on a grassy flat with prickly Acacia at Sangeang on 20 October 1988.

Hirundinidae

Hirundo rustica gutturalis Barn Swallow

Sumbawa I. – A flock of 25 circling Bima on 19 October 1988, common in small flocks in Teluk Sumbawa on 6 November 1988 and one at Babar, Selah Legium on 8 August 1993. These are the first records for Sumbawa.

Moyo I. – Moderately common in small flocks in and around Sebotok in November.

Sangeang I. – Two over village on 22 October.

Hirundo tahitica javanica Pacific Swallow

Sumbawa I. – Scarce. Ones and twos noted at Belo, Teluk Santong and Dompu in May and October 1988, and at Batu Hijau, Selah Legium, Maluku and 5 km east of Sumbawa Besar in August 1993.

Hirundo striolata Striated Swallow

Sumbawa I. – Only one record of four birds near Lake Taliwang on 9 August 1993.

Motacillidae

Anthus novaeseelandiae Richard's Pipit

Sumbawa I. – Locally moderately common in ones, twos and small groups (up to 6). Recorded at Teluk Santong and Sangeang. Coastal grassy flats.

Campephagidae

Coracina personata floris Wallacean Cuckoo Shrike

Sumbawa I. – Uncommon. Ones and twos. Recorded at Merente, near Alas, Belo, Batu Tering, Batu Hijau, Gunung Olet Sangenges and Batu Dulang. Mainly open woodland also lowland semi-evergreen rainforest.

Coracina dohertyi Sumba Cicadabird

Sumbawa I. – Status uncertain. Two at 250 m at RF2, Selah Legium on 5 August 1993, and frequent at 800–930 m at Gunung Olet Sangenges on 15–18 August 1993. All were in semi-evergreen rainforest. The first records for Sumbawa.

Lalage sueurii sueurii White-winged Triller

Sumbawa I. – Moderately common. Mainly in ones and twos. Recorded at Alas, Belo, Maluku Sumbawa Besar, 5 km east of Sumbawa Besar, Batu Tering, Teluk

Santong, Waworada and Sangeang. Mangal, coastal scrub, woodlands and cultivated areas.

Moyo I. – One in mangal at Sebotok on 7 November.

Sangeang I. – Pair in open woodland on 21 October and one on 22 October 1988.

Pericrocotus lansbergei Little Minivet

Sumbawa I. – Locally moderately common but generally uncommon. Recorded at Gunung Olet Sangenges, at three sites at Selah Legium and 5 km east of Sumbawa Besar. Mainly open parkland with some large trees and sparse understorey, also semi-evergreen forest, moist deciduous monsoon forest and riverine forest. Recorded up to 1150 m but most frequent below 500 m. Three males from Batu Dulang in MZB collection.

Laniidae

Lanius cristatus Brown Shrike

Moyo I. – A male collected from open woodland at Sebotok on 8 November 1988. Presumably a vagrant from northern Asia. The first record for the Sumbawa region.

Lanius schach bentet Long-tailed Shrike

Sumbawa I. – Moderately common. Recorded at Sumbawa Besar, Empang, Teluk Santong, Waworada and Sangeang. Also along northern coast from Maluku, through Taliwang and Sumbawa Besar to Sape. Open woodland and cultivated areas.

Saxicola caprata fruticola Pied Bushchat

Sumbawa I. – Locally moderately common in ones and twos. Recorded at Sumbawa Besar, Meraran, Belo, Babar, northern and western coasts from Maluku to Sape, Dompu, Waworada and Wawo. Mainly open coastal habitats, cultivated areas and edges of wetlands.

Moyo I. – Scarce. Recorded at Labuan Aji, Sebotok and Tanjung Pasir. Open woodland and prickly coastal scrub.

Sangeang I. – Scarce. Open scrub and village gardens.

Turdidae

Zoothera interpres Chestnut-capped Thrush

Sumbawa I. – Scarce or uncommon. Only recorded at Gunung Olet Sangenges and a single record from Batu Hijau, Selah Legium. Mainly lowland semi-evergreen forest and lower montane forest from 450 m to 850 m. Birds were in full song in July–August 1993 and a juvenile seen on 14 August. Apparently replaced by *Z. dohertyi* at higher altitude.

Zoothera dohertyi Chestnut-backed Thrush

Sumbawa I. – Locally moderately common but generally rare. Rare at Batu Hijau, Selah Legium and below 500 m at Gunung Olet Sangenges, but common above this altitude at the latter site. Mainly closed-canopy semi-evergreen forest with fruiting trees between 750 and 950 m. Rarely in degraded forest. Birds were singing in July–August. A female from Batu Dulang in MZB collection.

Zoothera andromedae Sunda Thrush

Sumbawa I. – One at 450 m in closed semi-evergreen forest at Batu Hijau, Selah Legium and four (including two mist-netted) at 550–850 m at Gunung Olet Sangenges in August 1993. These are the first records for Sumbawa.

Sylviidae*Tesia everetti sumbawana* Russet-capped Tesia

Sumbawa I. – Locally common. Only recorded at Batu Dulang, Gunung Olet Sangenges and at Batu Hijau and RF2, Selah Legium. Recorded from 200 m to 1700 m though slightly less common at higher altitudes. Favours the dense undergrowth of rainforest, bamboo thickets and dense riverine forest. Individuals were observed carrying nesting material at Batu Hijau on 29 July 1993.

Acrocephalus stentoreus Clamorous Reed Warbler

Sumbawa I. – Only recorded at Meraran wetlands where it was moderately common in Typha and lilies. An adult male collected on the 14 May had a weight of 21 g, total length 119 mm and wing 77 mm. It has a heavier bill and is paler and more streaked on the throat and breast than Western Australian populations.

Phylloscopus borealis Arctic Warbler

Sumbawa I. – Two males in MZB collection.

Phylloscopus trivirgatus trivirgatus Mountain Leaf-Warbler

Sumbawa I. – Three feeding in canopy of rainforest at Batu Dulang 1150 m on 3 November 1988.

Seicercus montis Yellow-breasted Warbler

Sumbawa I. – One feeding in canopy of rainforest at Batu Dulang 1150 m on 4 November. First record for Sumbawa.

Cisticola juncidis Zitting Cisticola

Sumbawa I. – Two adults and 3 fledged chicks in tall grass at Teluk Santong on 23 May 1988 and one in grassland at Sumbawa Besar on 10 August 1993. Also a specimen in MZB collection from Wawo.

Moyo I. – Moderately common in tall grass and coastal scrub at Tanjung Pasir.

Sangeang I. – Several in spinifex, grass and low shrubs near beach.

Muscicapidae*Rhinomyias oscillans* Russet-backed Rhinomyias

Sumbawa I. – Rare. Only recorded at Batu Hijau, Selah Legium between 27 July and 8 August 1993 in primary semi-evergreen forest from 500–650 m. Juveniles observed on 28 July and 2 August indicating breeding. Birds were not distinguishable from those on Flores and are presumably of the same race *R. o. oscillans*. The first records for Sumbawa.

Ficedula hyperythra vulcani Snowy-browed Flycatcher

Sumbawa I. – One in rainforest at Batu Dulang, 1150 m, on 4 November 1988.

Ficedula dumetoria dumetoria Rufous-chested Flycatcher

Sumbawa I. – Rare or uncommon. Recorded at Batu Hijau, Selah Legium, and at Gunung Olet Sangenges. Also a male from Batu Dulang in MZB collection. Mainly closed-canopy semi-evergreen forest above 400 m.

Monarchidae*Terpsiphone paradisi floris* Asian Paradise Flycatcher

Sumbawa I. – A male from Dompu in MZB collection.

Hypothymis azurea prophata Black-naped Monarch

Sumbawa I. – Moderately common throughout the island. Rainforest including moist deciduous monsoon forest, riverine forest, woodland, mangal, bamboo thickets and cultivated areas, below 1000 m. Forages mainly in lower levels of vegetation. Breeding – pair building a nest 6 m up in a bamboo thicket at Batu Tering on 26 May and a pair building 1.5 m up on a hanging vine at Dahu on 30 October.

Moyo I. – Moderately common. Recorded at Sebotok and Tanjung Pasir. Mangal, vine forest and woodland.

Sangeang I. – A female collected from a coastal *Ficus* thicket on 22 October.

Rhipiduridae*Rhipidura diluta sumbawensis* Brown-capped Fantail

Sumbawa I. – Locally moderately common e.g. at Waworada, Batu Dulang, Selah Legium and Gunung Olet Sangenges (up to 1700 m). Recorded in all forest types, including heavily degraded habitat. Most frequent in forest with an extensive understorey, along streams and in small clearings with dead vegetation lying on the ground.

Sangeang I. – One in a *Ficus* thicket near coast on 22 October.

Pachycephalidae*Pachycephala pectoralis fulvotincta* Common Golden Whistler

Sumbawa I. – Common to moderately common. Recorded at Merente, Belo, Selah Legium, Gunung Olet Sangenges, Batu Tering, Batu Dulang, Waworada, Dahu and Dompu. All forest habitats from 20–850 m including rainforest, bamboo thickets and cultivated areas.

Sangeang I. – Scarce. Pair in open scrub along a creek on 22 October.

Pachycephala nudigula ilsa Bare-throated Whistler

Sumbawa I. – Common in semi-evergreen forest at Batu Hijau and RF2, Selah Legium, and at Gunung Olet Sangenges during July–August 1993. Recorded from 200–1700 m. Mainly montane and riverine forest. Tolerant of habitat degradation only where the forest retained a closed canopy. This subspecies is endemic to Sumbawa.

Paridae*Parus major cinereus* Great Tit

Sumbawa I. – Scarce. Ones and twos. Recorded at

Gunung Olet Sangenges, Batu Tering, Batu Dulang, Waworada and Sangeang. Mainly open woodland, village gardens, also semi-evergreen rainforest, moist deciduous monsoon forest and scrub with scattered trees.

Dicaeidae

Dicaeum annae Golden-rumped Flowerpecker

Sumbawa I. – Locally moderately common but generally scarce or uncommon. Recorded at three sites at Selah Legium, also at Gunung Olet Sangenges, Merente, near Alas and at Batu Dulang. Mainly closed canopy semi-evergreen rainforest also cultivated areas with patches of rainforest. Recorded from 40 m to 1530 m, most frequent below 1000 m. Three birds with brood patches were mist-netted in early August, indicating breeding.

Dicaeum agile Thick-billed Flowerpecker

Sumbawa I. – Uncommon. Recorded at Batu Hijau, Selah Legium, at Gunung Olet Sangenges and at Babar in July–August 1993. Noted from 50–700 m and most records were from moist deciduous monsoon forest and scrub with scattered trees. The first records for Sumbawa.

Dicaeum igniferum Black-fronted Flowerpecker

Sumbawa I. – Common to moderately common. Recorded at Merente, three sites at Selah Legium, Gunung Olet Sangenges, near Alas, Batu Tering, Batu Dulang and Teluk Santong. Noted from 50–1730 m but rare in upper montane forest. Rainforest, degraded forest, monsoon forest, cultivated areas and woodland. Breeding noted in July–August 1993.

Moyo I. – Uncommon. Ones and twos recorded at Sebotok and Tanjung Pasir. Mangal, rainforest and open coastal scrub.

Nectariniidae

Anthreptes malacensis convergens Brown-throated Sunbird

Sumbawa I. – Moderately common. Recorded at Merente, Batu Hijau, Babar, Gunung Olet Sangenges, near Alas, Meraran, Teluk Santong, Batu Tering, Dahu and Domp. Mainly riverine forest, cultivated areas and scrub, less frequent in semi-evergreen forest. Noted from 20–1000 m.

Moyo I. – Uncommon. Two at Sebotok on 7 November.

Nectarinia jugularis ornata Olive-backed Sunbird

Sumbawa I. – Common. Recorded at Sumbawa Besar, Merente, Batu Hijau, Babar, footslopes of Gunung Olet Sangenges, near Alas, Belo, Batu Dulang, Batu Tering, Teluk Santong, Sangeang, Waworada and Dahu. Mainly cultivated areas, edges of rainforest, logged forest, riverine forest and open woodland.

Moyo I. – Scarce. Ones and twos at Amanwana, Sebotok and Tanjung Pasir. Cultivated areas and creekside forest. Also attracted to flowering *Erythrina*.

Sangeang I. – Scarce. Open woodland.

Nectarinia solaris Flame-breasted Sunbird

Sumbawa I. – Scarce. Recorded near Sumbawa Besar, Merente, three sites at Selah Legium, Gunung Olet Sangenges, near Alas and at Dahu. Mainly cultivated areas, riverine forest and degraded forest. Attracted to flowering *Kurrajong* and *Erythrina*. Juveniles observed in July–August.

Zosteropidae

Zosterops palpebrosus unicus Oriental White-eye

Sumbawa I. – Very common to moderately common in small flocks (up to 20) at Batu Dulang and Gunung Olet Sangenges. Lower and upper montane semi-evergreen forest from 850–1730 m.

Zosterops montanus Mountain White-eye

Sumbawa I. – Six recorded at 1500–1700 m in semi-evergreen montane forest at Gunung Olet Sangenges on 16 August 1993.

Zosterops wallacei Yellow-spectacled White-eye

Sumbawa I. – Locally moderately common. Recorded at Merente, three sites at Selah Legium, Gunung Olet Sangenges, Batu Tering, Batu Dulang, Domp. and Wawo. From 20–800 m in cultivated areas, bamboo thickets, scrub, forest-edge and heavily degraded forest. Tolerant of very dry habitat.

Moyo I. – Uncommon. Recorded at Sebotok and Tanjung Pasir. Vine forest and woodland.

Zosterops chloris intermedius Lemon-bellied White-eye

Sumbawa I. – Common in small flocks (up to 5). Recorded at Batu Tering, Batu Dulang, Teluk Santong, Sangeang, Waworada and Bima. Cultivated areas, mangal and open woodland.

Moyo I. – Common at Sebotok and Tanjung Pasir. Cultivated areas, coastal thickets and vine forest.

Sangeang I. – Common. Mainly small flocks. Open coastal woodland especially thickets of *Ficus*.

Lophozosterops superciliaris hartertianus Yellow-browed Darkeye.

Sumbawa I. – Common in upper montane semi-evergreen forest between 1400 and 1700 m at Gunung Olet Sangenges in August 1993. Also a female from Batu Dulang in MZB collection. Presumably common in remaining montane forests on Sumbawa.

Lophozosterops dohertyi dohertyi Crested Darkeye

Sumbawa I. – Locally common but generally scarce. Recorded at Batu Dulang, Batu Hijau, Gunung Olet Sangenges and RF2 (Selah Legium). Common at sites with closed-canopy semi-evergreen rainforest between 300 and 1400 m. Only found in degraded forest where a closed canopy and extensive understorey remained. Appears to be replaced by the congeneric Yellow-browed Darkeye above 1200 m. Breeding recorded in July–August 1993.

Heleia crassirostris Thick-billed Darkeye

Sumbawa I. – Locally moderately common. Recorded at three sites at Selah Legium and at Gunung Olet

Sangenges in July–August 1993. Noted from 100–1200 m. Most frequent in primary semi-evergreen rainforest and moist deciduous monsoon forest. Also in degraded forest-edge habitat and dry forest. Five mist-netted birds had brood patches and one bird was observed carrying nesting material in early August.

Estrildidae

Taeniopygia guttata guttata Zebra Finch

Sumbawa I. – Moderately common in small flocks (up to 10). Recorded at Sumbawa Besar, Belo, Batu Tering, Teluk Santong and Sangeang. Cultivated areas, open woodland and thickets of prickly Acacia.

Erythrura hyperythra intermedia Tawny-breasted Parrot-Finch

Sumbawa I. – Status uncertain. Three males from Sumbawa in MZB collection.

Lonchura molucca Black-faced Munia

Sumbawa I. – Common. Mainly in small flocks (up to 20) occasionally larger flocks up to 200. Recorded at Sumbawa Besar, Merente, Meraran, Belo, Maluku, Alas, footslope of Gunung Olet Sangenges, Batu Tering, Batu Dulang, Teluk Santong, Waworada and Dahu. Cultivated areas especially rice fields, edges of wetlands, edges of forest and lowland scrub. Breeding recorded in May.

Moyo I. – Uncommon to moderately common in small flocks (up to 8). Recorded at Sebotok and Brang Kua. Coastal thickets and edges of forest.

Lonchura punctulata nisoria Scaly-breasted Munia

Sumbawa I. – Common. Mainly small flocks (up to 30). Recorded at Sumbawa Besar, Belo, Teluk Santong, Waworada and Dahu. Mainly in and around rice fields.

Lonchura pallida Pale-headed Munia

Sumbawa I. – Uncommon. Mainly small flocks (up to 20). Recorded near Sumbawa Besar, Meraran, Maluku and Teluk Santong. Cultivated areas except at Meraran they were mostly in *Typha*, *Pragmites* and lilies.

Padda oryzivora Java Sparrow

Sumbawa I. – Uncommon. Flock of six on road near Sumbawa Besar on 8 May; four bathing in creek at Batu Tering on 26 May; and several in gardens at Batu Tering on 27 May 1988.

Meliphagidae

Philemon buceroides neglectus Helmeted Friarbird

Sumbawa I. – Common. Recorded at Merente, three sites at Selah Legium, Gunung Olet Sangenges, near Alas, Belo, Batu Tering, Batu Dulang, Dahu and Waworada. Rare above 1000 m. Rainforest, vine forest and cultivated areas.

Moyo I. – Common. Recorded at Sebotok, Brang Kua and Tanjung Pasir. Mangal, open woodland, rainforest and vine forest. Attracted to flowering *Sesbania*.

Sangeang I. – Common. Open woodland and creekside vegetation. Attracted to fruiting *Ficus*.

Lichmera lombokiana Scaly-crowned Honeyeater

Sumbawa I. – Only recorded at Gunung Olet Sangenges in August 1993. Common in upper montane semi-evergreen forest from 1000–1700 m and uncommon in lower montane forest (800–1000 m).

Lichmera indistincta limbata Brown Honeyeater

Sumbawa I. – Common. Recorded at Sumbawa Besar, Alas, Meraran, Batu Tering, Batu Dulang and Teluk Santong. Mangal and cultivated areas.

Sangeang I. – Common. Open woodland, vine scrub along creeks and cultivated areas.

Passeridae

Passer montanus Eurasian Tree Sparrow

Sumbawa I. – Moderately common to common. Recorded at Sumbawa Besar, Meraran, Belo, Maluku, Batu Tering, Bima and Sangeang. Town gardens cultivated areas and edges of swamps. Not listed by White and Bruce (1986) for Sumbawa and thought to be a recent introduction.

Sangeang I. – Uncommon. Recorded in open woodland near villages.

Sturnidae

Aplonis minor Short-tailed Starling

Sumbawa I. – Rare. Recorded between 200 m and 1600 m at Batu Hijau and at Gunung Olet Sangenges in July–August 1993.

Gracula religiosa venerata Hill Myna

Sumbawa I. – Uncommon. Two in a bamboo thicket edge of rainforest at Batu Dulang on 5 November 1988, also recorded at Batu Hijau, Selah Legium in semi-evergreen rainforest (450–650 m) in July–August 1993.

Moyo I. – Moderately common at Brang Kua and Tanjung Pasir. Attracted to fruiting trees especially *Ficus*.

Oriolidae

Oriolus chinensis broderipii Black-naped Oriole

Sumbawa I. – Common to moderately common in ones and twos. Recorded at Meraran, Belo, Batu Hijau, Babar, Gunung Olet Sangenges, Batu Tering, Batu Dulang and Dahu. Mainly lowland semi-evergreen and moist deciduous monsoon forest, riverine forest, woodland and bamboo thickets. Attracted to fruiting trees especially *Ficus* and *Eugenia* spp.

Moyo I. – Moderately common in ones and twos. Recorded at Sebotok, Brang Kua and Tanjung Pasir. Rainforest, woodland and mangal. Attracted to fruiting *Ficus* and *Eugenia*.

Sangeang I. – Moderately common in ones and twos. Vine forest.

Dicruridae

Dicrurus densus bimaensis Wallacean Drongo

Sumbawa I. – Moderately common throughout the island. Mainly in ones and twos and occasionally in small groups (up to 6). All lowland forests including

rainforest, riverine forest, vine thickets and cultivated areas. Rare in upper montane forest (up to 1430 m). Attracted to fruiting trees especially *Ficus* and *Terminalia*. Breeding; a nest with hatchlings at Dahu on 31 October.

Moyo I. – Moderately common in ones, twos and small groups (up to 8). Recorded at Amanwana, Labuan Aji, Sebotok, Brang Kua and Tanjung Pasir. Rainforest, coconut groves and low open woodland. Breeding; pair building a nest in huge leafless tree at Brang Kua on 10 November.

Sangeang I. – One in open woodland and three in a *Ficus* in October.

Artamidae

Artamus leucorhynchus albiventer White-breasted Woodswallow

Sumbawa I. – Moderately common in small groups (up to 20). Recorded at Sumbawa Besar, Belo, Lake Taliwang, Batu Dulang, Teluk Santong, Waworada, Dompu and Dahu. Mangal, edges of wetlands, open woodland and cultivated areas especially coconut groves.

Moyo I. – Moderately common at Sebotok and Brang Kua in small groups (up to 8). Mangal and cultivated areas.

Corvidae

Corvus macrorhynchos macrorhynchos Large-billed Crow.

Sumbawa I. – Uncommon or scarce. Ones and twos. Recorded at Teluk Santong, Empang, Sumbawa Besar and Babar. Mainly open woodland, coconut plantations, scrub and riverine forest.

Moyo I. – Scarce. Only recorded in coconut plantations at Sebotok.

DISCUSSION

A total of 162 (103 non-passerine and 59 passerine) were recorded on Sumbawa Island, 70 species (52 non-passerine and 18 passerine) on Moyo Island and 33 species (20 non-passerine and 13 passerine) on Sangeang Island. Of these 37 species are new records for the Sumbawa region namely: Lesser Frigatebird *Fregata ariel*, Little Pied Cormorant *Phalacrocorax melanoleucos*, Brown Booby *Sula leucogaster*, Little Egret *Egretta garzetta*, Striated Heron *Butorides striatus*, Yellow Bittern *Ixobrychus sinensis*, Lesser Adjutant *Leptoptilos javanicus*, Oriental Honey-buzzard *Pernis ptilorhynchus*, Black-winged Kite *Elanus caeruleus*, Black Kite *Milvus migrans*, Japanese Sparrowhawk *Accipiter gularis*, Rufous-bellied Eagle *Hieraaetus kienerii*, Australian Kestrel *Falco cenchroides*, Grey Teal *Anas gibberifrons*, Red-legged Rail *Rallina fasciata*, Purple Swampphen *Porphyrio porphyrio*, Grey Plover *Pluvialis squatarola*, Great Sand Plover *Charadrius leschenaultii*, Far-Eastern Curlew *Numenius madagascariensis*, Bar-tailed Godwit

Limosa lapponica, Common Redshank *Tringa totanus*, Terek Sandpiper *Xenus cinereus*, Grey-tailed Tattler *Heteroscelus brevipes*, Beach Thick-knee *Esacus magnirostris*, Little Tern *Sterna albifrons*, Great Crested Tern *Sterna bergii*, Lesser Crested Tern *Sterna bengalensis*, White Tern *Cygis alba*, Dark-backed Imperial Pigeon *Ducula lacermulata*, White-throated Needletail *hirundapus caudacutus*, Asian Palm-swift *Cypsiurus balasiensis*, Sumba Cicadabird *Coracina dohertyi*, Sunda Thrush *Zoothera andromedae*, Yellow-breasted Warbler *Seicercus montis*, Russet-backed Rhinomyias *Rhinomyias oscillans*, Thick-billed Flowerpecker *Dicaeum agile* and Tree Sparrow *Passer montanus*.

A further 7 species are listed for Sumbawa by White and Bruce (1986) namely: Greater Painted Snipe *Rostratula benghalensis*, Common Greenshank *Tringa nebularia*, Lesser Shortwing *Brachypteryx leucophrys*, Little Pied Flycatcher *Ficedula westernmanii*, Island Monarch *Monarcha cinerascens*, Grey Wagtail *Motacilla cinerea* and Five-coloured Munia *Lonchura quincolor*.

Of these the Greater Painted Snipe is scarce and local in the Lesser Sundas; Common Greenshank and Grey Wagtail are both winter visitors from the Palearctic; Lesser Shortwing and Little Pied Flycatcher are largely confined to montane forest over 1000 m, appear to be very local in distribution and possibly confined to vicinity of Gungung Tambora; and the Island Monarch and Five-coloured Munia also appear to be fairly localised in their distribution.

Combining all records gives a total of 179 species for Sumbawa and its satellite islands. For its size and position Sumbawa has a relatively impoverished fauna when compared with Lombok 4,700 km² with about 150 species and Flores 17,000 km² with about 215 species. Few additional passerine species could be expected for Sumbawa, however more work along the coast would no doubt add many visiting waders to the list. Additional wetland birds could also be expected during visits after good seasons.

The avifauna of Sumbawa, Moyo and Sangeang Islands is typical of the western Lesser Sunda Islands having much in common with Lombok Island to the west and Flores to the east. The depauperate fauna of Sumbawa when compared to the similar sized Flores Island is no doubt partly due to the comparatively arid conditions that prevail over most of the island, especially the eastern half, and the lack of variety of habitats in general. Sumbawa does however support a number of species with high conservation importance including many listed as threatened or near threatened in Collar *et al.* (1994) namely: Flores Green Pigeon, Nicobar Pigeon, Yellow-crested Cockatoo, Wallace's Scops Owl, Sumba Cicadabird, Russet-backed Rhinomyias and

Crested Darkeye. The Flores Green Pigeon and Nicobar Pigeon favour small islands. Both are very localised in distribution and are the target of trappers. The Yellow-crested Cockatoo is now very rare on Sumbawa and moderately common on Moyo Island. On Sumbawa it has declined greatly through habitat destruction and persecution for the cage bird trade. Wallace's Scops Owl is restricted to Sumbawa and Flores and appears to be rare on both islands. The Sumba Cicadabird was previously only known from Sumba and Flores, and the Sumbawa birds may represent an undescribed subspecies Butchart *et al.* (1993). The Russet-backed Rhinomyias was also only previously known from Flores and Sumba and records from Sumbawa are an important extension of range. The Crested Darkeye is restricted to Sumbawa and Flores and like the Russet-backed Rhinomyias occurs mainly in mid-level semi-evergreen rainforest. Mid-level forest is being destroyed at an alarming rate on both Flores and Sumbawa and both species do not appear to tolerate degraded forest.

Overall Sumbawa shares eight endemic species with Flores namely: Wallace's Scops Owl, Little Minnivet, Russet-capped Tesia, Bare-throated Whistler, Golden-rumped Flowerpecker, Yellow-browed Darkeye, Thick-billed Darkeye and Crested Darkeye. Sumbawa also contains six endemic subspecies namely: *Trichoglossus haematodus forsteni*, *Tesia everetti sumbawana*, *Rhipidura diluta sumbawensis*, *Pachycephala nudigula ilsa*, *Lophozosterops superciliosus hartertianus* and *Lophozosterops dohertyi dohertyi*.

Mayr (1944) and White and Bruce (1986) showed that from Bali east through the Lesser Sunda Islands to Alor there is a progressive decrease in birds of Asian affinities and an increase in species with Australian affinities. Sumbawa lies in this transitional zone between the Oriental and Australasian faunas. Although primarily Oriental the avifauna of Sumbawa contains a small Austro-Papuan element including the Grey Teal, Red-cheeked Parrot, Rainbow Lorikeet, Rainbow Bee-eater, Brown Honeyeater and Zebra Finch.

The migrant species visiting Sumbawa, Moyo and Sangeang can be divided into three main groups:

1. Non-breeding winter visitors from the Palearctic e.g. Grey Plover *Pluvialis squatarola*, Red-necked Phalarope *Phalaropus lobatus*, Common Sandpiper *Tringa hypoleucos*, Spine-tailed Swift *Hirundapus caudacutus* and Barn Swallow *Hirundo rustica*;
2. Passage migrants including many waders e.g. Grey-tailed Tattler *Tringa brevipes* and Bar-tailed Godwit *Limosa lapponica*;
3. Winter visitors from Australia including

Australian Pelican *Pelecanus conspicillatus* and Rainbow Bee-eater *Merops ornatus*;

4. South-east Asian migrants including the Lesser Adjutant *Leptoptilos javanicus* and Brown Shrike *Lanius cristatus*.

The faunas of Moyo and Sangeang Islands are of interest because they would have been derived almost wholly from Sumbawa Island, and in both cases would have a history of extinction and acquisition caused by catastrophic volcanic eruptions. The massive eruption of Gunung Tambora in 1815 would almost certainly have devastated all the vegetation on Moyo Island, and the eruption of Gunung Api on Sangeang Island in 1986 appears to have destroyed or burnt most of the vegetation there. A total of 70 species were recorded on Moyo Island, comprising 52 species of non-passerine and 18 species of passerine, and 33 species on Sangeang comprising 19 non-passerine and 14 passerine species. Two additional species the Brahminy Kite *Haliastur indus* and the Great Tit *Parus major* are listed for Sangeang by Bruce (1987) from a brief visit of the yacht 'Marchesa' (Guillemard 1885).

On Moyo Island as on many other Lesser Sunda Islands non-passerine species outnumber passerines by a ratio of about 2:1. An examination of the species lists for these islands immediately shows which species are successful colonists. Many species of bird are reluctant crossers of even the narrowest stretches of water, whereas others regularly cross water gaps of many kilometres (Diamond 1974). Discounting the migrant species on both islands, the lists comprise entirely of lowland species that have colonised not only these islands but many others in the Lesser Sundas. One interesting omission from Moyo Island is the Golden Whistler. This species is widespread and moderately common on Sumbawa Island and has successfully colonised hundreds of other oceanic islands.

ACKNOWLEDGEMENTS

We thank Mr N. Kolichis whose grants to the Western Australian Museum defrayed the costs of R.E. Johnstone's two field expeditions to Sumbawa. We are also grateful to B.R. Lees for bird observations from Moyo Island.

We gratefully acknowledge the support given to us by our Institutions, the Western Australian Museum (WAM), Perth, and the Museum Zoologicum Bogoriense (MZB), Bogor. We also thank the past and present Directors Dr S. Kadarsan and Dr Soetikno Wirioatmodjo respectively, of Puslitbang Biologi, Lembaga Ilmu Pengetahuan Indonesia and Dr D.J. Kitchener of the Western Australian Museum for facilitating this collaborative project.

SHMB and JCL gratefully acknowledge their co-expedition members for support and advice: Tom Brooks, Charles Davies, Gunawan Dharmaputra, Alo Sahu, and particularly Guy Dutton. The Cambridge Flores/Sumbawa Conservation Project 1993 would like to thank the Earl of Cranbrook, Rudyanto, Priyo Budy Asmoro, Bas van Balen, Roger Barnes, Yusup Cahyadin, Cambridge University Explorers' and Travellers' Club, Dr David Chivers, Peter Colston, Rob Clay, Mike Crosby, Carl Downing, Jonathan Eames, Tom Evans, Dave Gandy, Rob Giles, Derek Holmes, Agil al Idrus, Carol Inskip, Dr Martin Jones, Ben King, Dr Frank Lambert, Durwyn Liley, Richard Lindsay, Anda Lisa, Dr Kathy MacKinnon, Dr Kathryn Monk, Dr Jim Paine, Dewi Praistuti, Wahyu Raharjaningtrah, Richard Ranft, Irinus Ros, Paul Salaman, Nat Seddon, Jeni Shannaz, Dr Marcel Silvius, Steve Smith, Tony Stones, Sujatnika, Rob Timmins, Joe Tobias and Nigel Winner.

The expedition was generously supported by: Bird Exploration Fund, BirdLife International/FFPS BP Conservation Expedition Competition, British Ornithologists' Union, A.S. Butler Charitable Trust, Cambridge Expeditions Fund, Chadwyck-Healey Ltd., Clare College, Emmanuel College, The Explorers' Club Youth Activity Fund, Fitzwilliam College, Russell and Mary Foreman 1980 Charitable Trust, Royal Geographical Society, Royal Society of St George, Gilchrist Educational Trust, J.R. Greenwood, Lindeth Charitable Trust, J.F. & E.A. Measures Charity, Newby Trust Ltd., Oriental Bird Club, PT Newmont Nusa Tenggara, The People's Trust for endangered Species, Peter Natham Charitable Trust, Shell International Petroleum Co. Ltd., L.E. Simmons (Chesterton Travel Group), SmithKline Beecham, Wexas International, Glaxo Group Research Ltd., Wildwings, Carl Zeiss Ltd and the sponsors of the National Student Bird Race.

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Morphological variation among eastern Indonesian island populations of *Hipposideros bicolor* (Chiroptera: Hipposideridae), with descriptions of three new subspecies

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Abstract – *Hipposideros bicolor* (Temminck, 1834) is recorded for the first time in the Indonesian Lesser Sunda islands of Sumbawa, Selaru, Sumba, Savu, Roti and Timor. Morphological comparisons of cranial, dentary, dental and external body characters and univariate and multivariate statistical analyses of measurements of these characters were carried out on 76 adult specimens from six islands in the Lesser Sundas and, for comparison, with specimens from Java and Peninsula Malaysia.

This study reveals that *H. bicolor* differentiates morphologically into three subspecies, which are described herein. These subspecies, and an indeterminate subspecies from Sumbawa island, are closer phenetically to *H. b. bicolor* from Java than to *H. b. atrox* from Peninsula Malaysia.

INTRODUCTION

Hill (1963) characterised the *Hipposideros bicolor* group by the following features: small to moderate body size; large broadly rounded ears, normally with an internal fold or thickening of the membrane of the ear at the antitragal lobe; elongate and narrow skull; unspecialised auditory region; upper incisors weak with outer lobe obsolescent or obsolete. The taxonomy of *H. bicolor* and closely related forms has been confused since the work of Andersen (1918). Hill in Corbett and Hill (1992) considered the *bicolor* group in the Indo-Malay region comprised 22 species.

Hill (1963), in his classical review of *Hipposideros*, recognised the following forms of *H. bicolor*:

<i>H. bicolor bicolor</i> (Temminck, 1834)	North West Java, Banka island
<i>H. b. javanicus</i> Sody, 1937	Central Java
<i>H. b. pomona</i> Andersen, 1918	Southern India
<i>H. b. gentilis</i> Andersen, 1918	North India, Sikkim, Burma
<i>H. b. sinensis</i> Andersen, 1918	South China, Hainan, Thailand, Indochina
<i>H. b. atrox</i> Andersen, 1918	Malay Peninsula, Terutau island, Tioman island, Sumatra
<i>H. b. major</i> Andersen, 1918	Enggano island

H. b. erigens Lawrence, 1939 Mindoro island
Philippines

H. b. macrobullatus Tate, 1941 South Sulawesi

Hipposideros javanicus was first placed in synonymy with *H. b. bicolor* by Tate (1941) and this was later supported by Hill (1983) following his examination of an additional Javanese specimen of this subspecies. Hill *et al.* (1986) stated that “the forms *pomona*, *gentilis* and *sinensis* were probably conspecific”. Hill in Corbett and Hill (1992) confirmed this and placed *gentilis* and *sinensis* as subspecies of *H. pomona*. Hill *et al.* (1986) agreed with Strien (1986) and Bergmans and van Bree (1986) that *H. macrobullatus* was a species. Hill in Corbett and Hill (1992) stated that *H. b. major* may be synonymous with *H. b. atrox*; he considered that in Indonesia the forms of *H. bicolor* were *H. b. atrox* (Nias and Enggano islands, Sumatra) and *H. b. bicolor* (Bangka island, Java, Flores island and possibly Timor island and Kangean island (Hill and Rozendaal 1989)). With regard to their presence on Timor island Goodwin (1979) examined three specimens from Tutuala, on the northeastern tip of East Timor, which he was unable to assign to subspecies.

Kitchener and Maharadatunkamsi (1995) described a unique form of *Hipposideros* of the *H. bicolor* group from Sumbawa island, based on a single skull and two carcasses. They could not confidently ascribe it to a species on the material available but it was closest to *H. bicolor* in overall

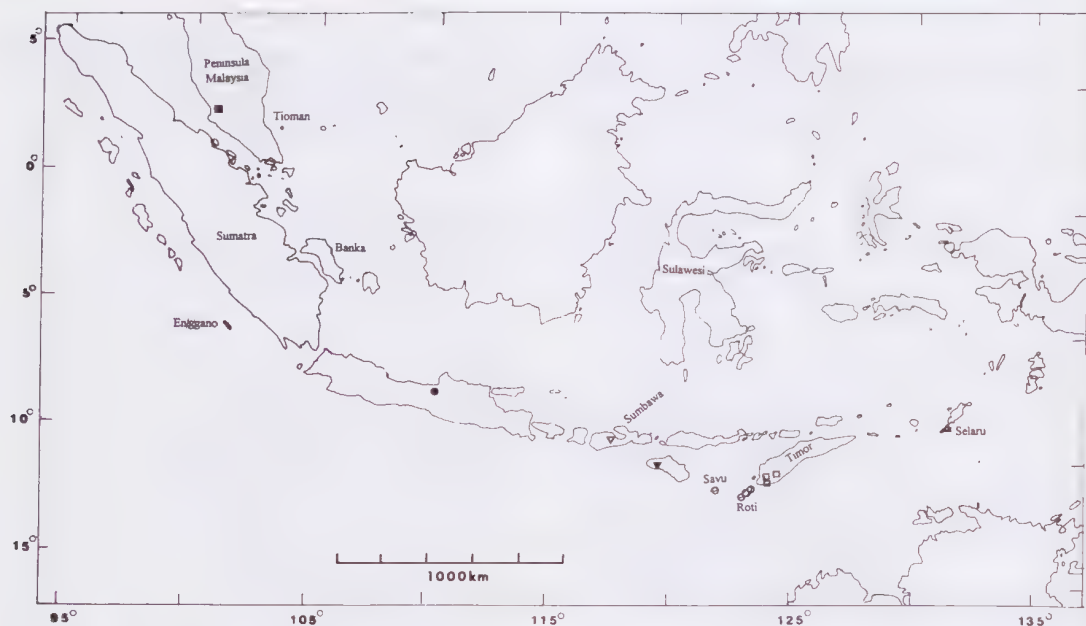


Figure 1 Locality of *Hipposideros bicolor* specimens used in this study, ■, *H. b. atrox*; ●, *H. b. bicolor*; △, *H. b. tanimbarensis* subsp. nov.; □, *H. b. hilli* subsp. nov.; ○, *H. b. selatan* subsp. nov.; ▽, *H. b.* subsp. indet. and ▼, Sumba specimen.

dimensions. *H. bicolor* is also reported from nearby Flores island by Hill and Rozendaal (1989).

More recently, collections of *H. bicolor* have been made from the following islands in the Lesser Sunda group: Selaru (Tanimbar Is), Timor, Roti, Savu, Sumba - see Figure 1 map. These specimens exhibit some morphological differences from the described forms of *H. bicolor*. This paper reports on an examination of this morphological variation, particularly that of taxonomic significance.

MATERIALS AND METHODS

76 adult specimens from six islands in the Lesser Sunda group and from Java and Peninsula Malaysia were measured.

Adult condition was judged by an absence of swelling of the epiphyseal joints of the wing metacarpals and phalanges.

The description of the colour of the pelage and patagia, where they follow Smithe (1975), are capitalised.

Measurements were as follows: GSL, greatest skull length; CB, braincase breadth; ZW, zygomatic width; MW, mastoid width; RL, rostrum length; LIB, least interorbital breadth; TBL, tympanic bulla length; ILD, interlachrymal distance; CL, cochlea length; CW, intercochlear distance; C¹B, upper canine breadth at base; P³B, second upper premolar cusp breadth; M³B, last upper molar cusp breadth; M¹M³L, upper molar row cusp length; C¹M³L,

upper canine to last upper molar cusp length; M²M³W, width across M² to M³ from outer alveoli edge; I₁M₃L, lower tooth row length; DL, dentary length; SVL, snout to vent length; TVL, tail to vent length; EL, ear length; TIL, tibia length; FA, forearm length; D2-5 MC, digits 2 to 5 metacarpal length; D3-5 P1, digits 3 to 5 phalanx 1 lengths; D3-5 P2, digits 3 to 5 phalanx 2 lengths; ANB, anterior noseleaf maximum breadth; PNB, posterior noseleaf maximum breadth.

Sexual dimorphism of all cranial, dentary, dental and body characters that were measured was investigated by standard multiple regression analyses (where all effects were assessed simultaneously of each character on sex and island). Graphical inspection of raw data using plots from regression analyses gave no indication of heteroscedasticity.

Stepwise Canonical Variate (Discriminant Function) analyses were run for all cranial, dentary, dental and external body characters measured for both sexes combined.

RESULTS

Multiple regressions

Localities included in these analyses were from Peninsula Malaysia, Java, Selaru, Timor, Roti, Savu and Sumba islands.

The analyses showed that there were no significant interactions between locality and sex for

Table 1 Multiple regressions on sex and localities (Peninsula Malaysia, Java, Sumbawa, Selaru, Timor, Roti, Savu and Sumba islands) of *Hipposideros bicolor* for (a) cranial, dentary and dental characters and (b) external body characters. F values are presented for the main effects only; there were no significant ($P<0.05$) interactions. For explanation of character codes see Materials and Methods section. Significance levels are *, $P<0.05$; **, $P<0.01$; and *** $P<0.001$.

Character	Sex	Locality
GSL	5.668*	9.054***
MW	2.069	2.067
RL	4.901*	3.936**
CW	0.005	3.839**
LIB	2.802	10.957***
CB	0.176	4.709**
TBL	0.063	0.941
ILD	0.232	16.740***
CL	1.139	0.384
M ³ M ³ W	5.792*	9.936***
C ¹ B	2.116	10.239***
P ³ B	0.065	4.266**
M ¹ M ³ L	0.008	0.044
M ² B	4.073	3.580**
C ¹ M ³ L	0.279	6.521***
DL	0.655	10.843***
I ₁ M ₃ L	1.673	6.254***
d.f.	1,41	6,41

Table 1(b)

Character	Sex	Locality
SVL	0.492	2.039
TVL	6.897*	3.571**
EL	0.123	4.110**
TIL	5.877*	1.441
FA	2.805	3.826**
D2MC	0.269	4.050**
D3MC	2.859	5.351***
D3P1	2.116	11.586***
D3P2	0.556	1.034
D4MC	2.513	5.141***
D4P1	5.675*	7.026***
D4P2	0.018	0.977
D5MC	0.751	4.521**
D5P1	5.718*	5.093***
D5P2	3.116	2.207
ANB	1.826	1.592
PNB	2.231	3.715**
d.f.	1,55	6,55

either cranial, dentary, dental or external body characters. However, the following characters were significantly sexually dimorphic at $0.05>P>0.01$: greatest skull length; rostrum length; outside M³-M³ width; tail to vent length; tibia length and both digit 4 and digit 5 phalanx 1 length. However, considering the number of interactions being tested, these were only weakly significant interactions (Table 1a, b).

Most cranial, dentary, dental and external body characters differed significantly at ($P<0.01$) with locality except: mastoid width; tympanic bulla length; cochlea length; upper molar row length; snout to vent length; tibia length; digits 3, 4 and 5 phalanx 2 length and anterior noseleaf breadth (Table 1a, b). This indicated the existence of considerable morphological variation among the populations. This variation is also apparent in the descriptive statistics presented in Table 2 for groupings of these island populations.

Discriminant Function Analysis (DFA)

Analyses of cranial, dentary and dental characters were run separately from those of external body characters. Both sexes were combined in these analyses. Characters excluded from the analyses were: zygomatic width (frequently damaged and some missing cases); greatest skull length; rostrum length; outside M³-M³ width; tail to vent length; tibia length; digit 4 phalanx 1 length and digit 5 phalanx 1 length (sexually dimorphic).

Initially, DFA were run for all characters, but because many of the groupings of populations had fewer individuals than there were characters measured, DFA in all cases were also run with a subset of five characters. These five characters were selected to provide values that minimised Wilk's lambda (How *et al.* 1996). In all cases the reduced set of five characters provided groupings of individuals in discriminant function space that were similar to those based on the complete set of characters. For this reason, only the DFA based on five characters are detailed below.

Cranial, dentary and dental characters

The DFA based on five characters (lachrymal breadth, least interorbital breadth, dentary length, P³ breadth and I₁M₃ length) and using as groups each island and the Peninsula Malaysia population, extracted three significant functions which indicated the presence of four putative groups as follows: Selaru; Timor; Roti/Savu; Peninsula Malaysia - with the few Java and Sumba specimens not clearly allocated (Figure 2a, b). The relatively high proportion (89.7%) of individuals that were classified to their correct locality indicated that these groups were robust.

The DFA based on the above four groups, with

Table 2b – external body characters

Island	Variable	SVL	TVL	EL	TIL	FA	D2MC	D3MC	D3P1	D3P2	D4MC	D4P1	D4P2	D5MC	D5P1	D5P2	ANB	PNB
<i>H.b. atrox</i> (Peninsula Malaysia)	\bar{x}	43.1	29.2	19.0	18.9	43.1	35.8	32.0	17.4	18.7	33.7	10.6	9.1	31.5	12.7	10.9	4.9	5.4
	S.D.	2.6	1.6	1.2	0.6	1.0	1.0	1.0	0.4	0.8	0.6	0.4	0.3	1.0	0.4	0.3	0.3	0.4
	Min	39.4	27.4	17.4	18.5	42.3	34.6	31.2	16.9	17.9	33.3	10.1	8.7	30.5	12.2	10.4	4.6	5.0
	Max	45.3	31.2	20.3	19.8	44.5	37.0	33.4	17.9	19.7	34.6	10.9	9.5	32.9	13.2	11.1	5.1	6.0
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4
<i>H.b. bicolor</i> (Java)	\bar{x}	48.2	31.1	19.0	20.7	44.8	36.8	34.4	18.4	18.6	36.6	11.0	9.0	34.8	13.4	11.7	4.6	4.8
	S.D.	0.5	1.0	0.2	0.4	0.1	0.8	0.1	0.9	1.5	0.5	0.2	0.6	0.5	0.3	0.8	0.4	0.1
	Min	47.8	30.4	18.8	20.4	44.7	36.2	34.3	17.8	17.6	36.2	10.9	8.6	34.5	13.2	11.1	4.3	4.7
	Max	48.5	31.8	19.1	21.0	44.8	37.3	34.4	19.0	19.7	36.9	11.2	9.4	35.2	13.6	12.3	4.8	4.9
	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>H.b.</i> subsp. indet. (Sumbawa)	\bar{x}	49.3	31.6	20.2	21.1	46.6	38.0	34.5	19.0	20.4	36.9	11.2	9.4	35.6	13.4	12.4	5.0	5.7
	S.D.	0.1	4.2	0.8	0.4	0.5	0.6	0.1	0.1	1.2	0.9	0.2	0.2	0.4	0.1	0.3	0	0
	Min	49.2	28.6	19.7	20.8	46.2	37.6	34.4	18.9	19.5	36.2	11.1	9.2	35.4	13.4	12.2	5.0	5.7
	Max	49.4	34.6	20.8	21.4	46.9	38.4	34.6	19.1	21.2	37.5	11.4	9.5	35.9	13.5	12.6	5.0	5.7
	N	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>H.b. tanimbarensis</i> (Selaru)	\bar{x}	45.1	32.2	20.6	19.4	42.9	35.9	32.5	18.0	18.8	35.0	10.4	9.1	33.5	12.6	11.5	4.8	5.6
	S.D.	1.8	2.3	0.6	0.5	1.0	0.8	0.5	0.5	1.0	0.6	0.3	0.4	0.7	0.4	0.4	0.3	0.2
	Min	41.8	27.2	19.5	18.5	40.3	34.5	31.0	17.2	15.4	33.6	1.0	8.5	32.0	12.1	10.8	4.1	5.1
	Max	48.2	35.5	21.8	20.5	45.0	37.5	33.3	18.9	19.8	36.4	11.0	9.8	34.9	13.3	12.3	5.2	5.9
	N	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	24	24
<i>H.b. hillii</i> subsp. (Timor)	\bar{x}	44.2	30.9	20.0	19.2	42.3	35.6	32.1	17.1	18.4	34.5	10.0	8.8	33.6	12.2	11.1	4.6	5.4
	S.D.	1.9	2.1	0.8	0.6	0.9	0.9	0.7	0.5	0.9	0.8	0.3	0.5	0.7	0.4	0.5	0.4	0.3
	Min	38.1	26.7	18.0	18.2	40.8	33.5	30.3	16.3	16.4	32.7	9.4	6.6	32.3	11.4	10.0	3.8	4.5
	Max	47.6	35.1	22.2	20.8	44.4	37.4	33.4	17.9	20.0	36.0	10.5	9.6	34.8	13.1	12.1	5.2	6.0
	N	34	31	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34
<i>H.b. selatan</i> subsp. nov. (Roti/Savu)	\bar{x}	45.4	32.1	20.6	19.2	42.7	34.8	31.7	17.2	18.9	33.5	10.2	9.0	33.0	12.6	11.2	4.8	5.8
	S.D.	1.0	2.3	0.5	0.5	0.8	0.7	0.8	0.7	0.9	0.8	0.4	0.6	0.8	0.5	0.4	0.3	0.4
	Min	44.5	29.0	19.6	18.5	41.6	34.0	30.4	16.1	17.2	32.0	9.5	8.3	31.7	11.9	10.5	4.5	5.4
	Max	47.3	35.6	21.4	19.8	43.7	35.8	33.0	18.1	20.0	34.6	10.6	10.3	33.8	13.2	11.8	5.2	6.5
	N	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	8
<i>H.b.</i> subsp. cf. <i>tanimbarensis</i> (Sumba)	N=1	43.1	36.5	20.8	20.6	45.1	38.6	34.9	18.1	19.9	36.8	10.6	9.4	35.6	13.1	12.4	4.9	5.9

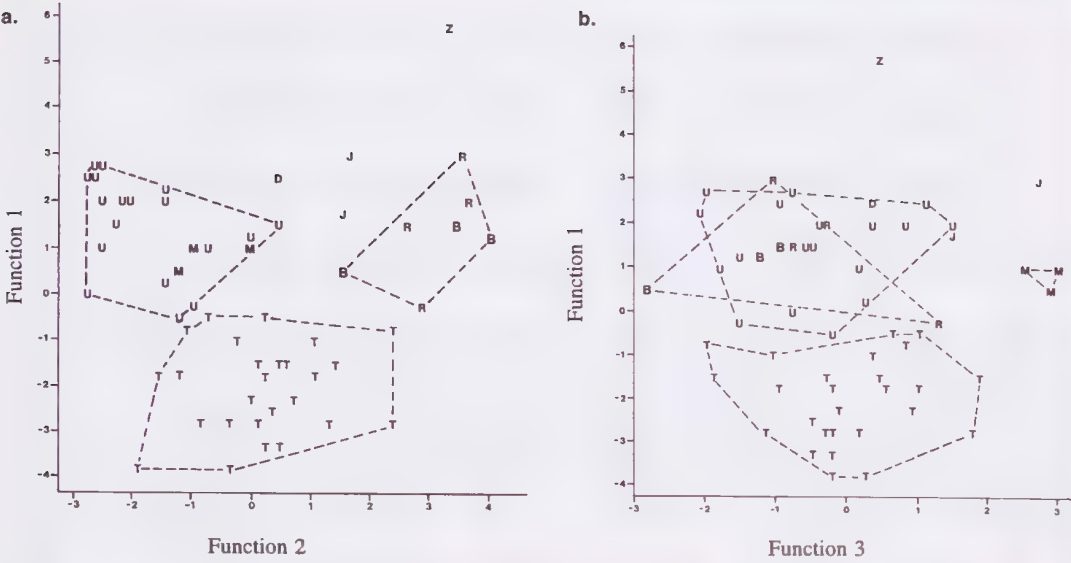


Figure 2 Canonical Variate Analysis among each island and the Peninsula Malaysia population of *Hipposideros bicolor* and based on a subset of five cranial, dentary and dental characters (see text). Population codes are as follows: B, Savu island; D, Sumba island; J, Java island; M, Peninsula Malaysia; R, Roti island; T, West Timor; U, Selaru island; and Z, Sumbawa island. (a) plots of Functions 1 and 2, and (b) plots of Functions 1 and 3.

Table 3 Canonical variate function coefficients from analysis based on four groupings of *Hipposideros bicolor* populations (Selaru, Timor, Roti/Savu and Peninsula Malaysia) and on a subset of five characters for (a) cranial, dentary and dental characters and (b) external body characters. See Materials and Methods for explanation of character codes.

Table 3a

Character	Function 1	Function 2	Function 3
ILD	-0.0567 (-0.7527)	1.0084 (13.3952)	-0.3758 (-4.9920)
DL	0.8646 (5.4397)	0.3208 (2.0181)	0.4812 (3.0276)
LIB	-0.5959 (-7.0866)	-0.0927 (-1.1022)	0.8110 (9.6452)
P ³ B	0.4464 (8.2084)	0.0402 (0.7392)	0.4569 (9.4022)
I ₁ M ₃ L	-0.1004 (-0.5628)	-0.6067 (-3.4003)	-0.2244 (-1.2573)
Constant	-42.7810	-57.2068	-36.7831
Variation explained (%)	56.8	35.3	7.9

Table 3b

Character	Function 1	Function 2	Function 3
D3P1	-0.8525 (-1.7123)	0.6319 (1.2693)	0.2407 (0.4834)
D5MC	1.5099 (2.0338)	0.3248 (0.4374)	0.5502 (0.7411)
FA	-0.5068 (-0.5340)	-0.5134 (-0.5410)	0.3127 (0.3294)
EL	0.3661 (0.4960)	0.5985 (0.8109)	0.4401 (0.5962)
D4MC	-0.3931 (-0.5320)	0.2409 (0.3259)	-1.3309 (-1.8010)
Constant	-6.9297	-41.3082	29.342
Variation explained (%)	60.2	27.2	12.6

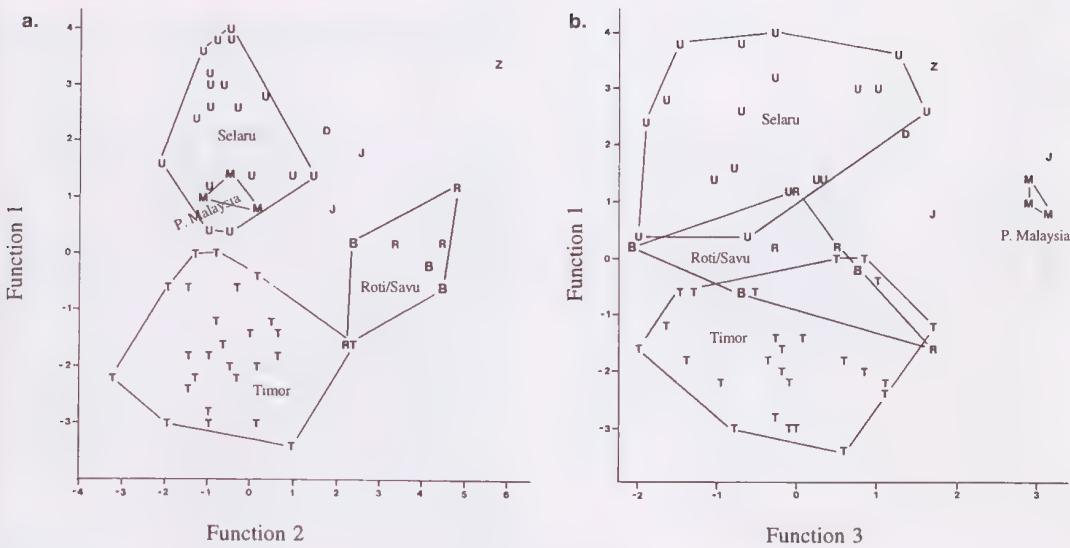


Figure 3 Canonical Variate Analysis among four population groupings of *Hipposideros bicolor* (Selaru, Timor, Roti/Savu and Peninsula Malaysia) - with the few Sumba, Sumbawa and Java specimens unallocated - and based on a subset of five cranial, dentary and dental characters (see text). (a) plots of Functions 1 and 2 and (b) plots of Functions 1 and 3. Population codes as for Figure 2.

the two Java specimens and single Sumba and Sumbawa specimens unallocated, and again using the above five characters, extracted three significant functions which allocated 98.2% of the specimens to their correct group. Function 1, which explained 56.8% of the variance, separated the Selaru and Malay Peninsula Group from the Timor Group (Figure 3a). The characters with high coefficients (>0.5) on Function 1 were dentary length and least interorbital breadth (Table 3a). Function 2 (35.3% of variance) separated the Roti/Savu Group from the Selaru, Malay Peninsula and Timor Groups (Figure 3a). The character with the highest coefficient (>0.5) on Function 2 was interlacrimal distance (Table 3a). Function 3 (7.9% of variance) separated the Malay Peninsula Group from the other three groups (Figure 3b). The character with the highest coefficient on Function 3 was least interorbital breadth (Table 3a). Of the unallocated specimens, one of the Javanese specimens allocated to the Peninsula Malaysia Group and the other to the Roti/Savu Group; the Sumba and Sumbawa specimens allocated to the Selaru Group.

External body characters

The DFA based on five characters (digit 3 phalanx 1 length, digit 4 metacarpal length, forearm length, ear length and digit 2 metacarpal length), and using as groups each island population and the Peninsula Malaysia population, extracted four significant functions but with only

61.8% of individuals classified to their correct locality. Bivariate plots of these functions did not reveal the discrete clusters apparent for the cranial, dentary and dental characters, although there was partial separation between the Timor and Selaru Groups (Figure 4).

A DFA was run based on five characters (digit 3 phalanx 1 length, digit 5 metacarpal length, digit 4 metacarpal length, ear length and forearm length) and using as groups those identified in the earlier cranial, dentary and dental analysis. This DFA extracted three significant functions with 80.3% of individuals classified to their correct groups. There was considerable overlap between the Timor and Selaru Groups, with 11.8% of individuals from the Timor Group misclassified to the Selaru Group. A total of 37.5% of the Roti/Savu Group were misclassified to either the Selaru Group (12.5%) or the Timor Group (25.0%). Of the ungrouped specimens, the two from Sumbawa and the two from Java grouped with the Selaru Group; the single specimen from Sumba island grouped with the Selaru Group. Only the Peninsula Malaysia Group was discrete. Function 1, which explained 60.2% of the variance, separated the Peninsula Malaysia Group from the other groups and from the unallocated Sumbawa, Java and Sumba specimens (Figure 5). The characters with high coefficients (> 0.5) on Function 1 were digit 5 metacarpal length, digit 3 phalanx 1 length and forearm length (Table 3b). Function 2 (27.2% of variance) also separated the Peninsula Malaysia

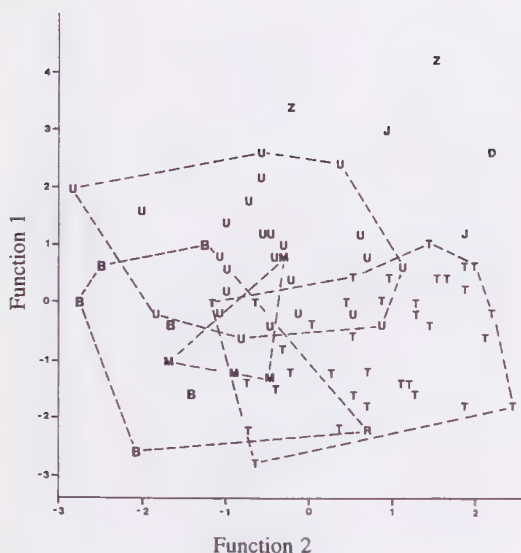


Figure 4 Plots of Functions 1 and 2 from Canonical Variate Analysis among each island population and the Peninsula Malaysia populations of *Hipposideros bicolor* and based on a subset of five external characters (see text). Population codes as for Figure 2.

Group from the Selaru Group and partially separated it from the Timor Group; it also partially separated the Timor and Roti/Savu Groups from the Selaru Group (Figure 5). The characters with high coefficients (>0.5) on Function 2 were digit 3 phalanx 1, ear length and forearm length. Function 3 (12.6% of variance) also separated the Malay Peninsula Group from the Roti/Savu Group. The characters with high coefficients (>0.5) on Function 3 were digit 4 and 5 metacarpal lengths (Table 3b).

In summary, the above statistical analyses indicated that the specimens of *H. bicolor* from the Lesser Sunda islands differed morphologically in both cranial, dentary, dental and external body characters from *H. bicolor atrox* from Peninsula Malaysia and also on cranial, dentary and dental characters from *H. b. bicolor* from Java. However, among this island chain the populations were further differentiated on cranial, dentary and dental characters into three clear forms (Timor, Selaru and Roti/Savu). The two Sumbawa island specimens grouped closely with those from Selaru island on external body morphology but on cranial, dentary and dental morphology the single specimen available for study was not closely associated with any of the other specimens. The Sumba island specimen is clearly closely associated with the Selaru form on cranial, dentary and dental characters and is tentatively referred to that form. The Sumbawa specimens, described in detail by Kitchener and Maharadatunkamsi (1995), are not

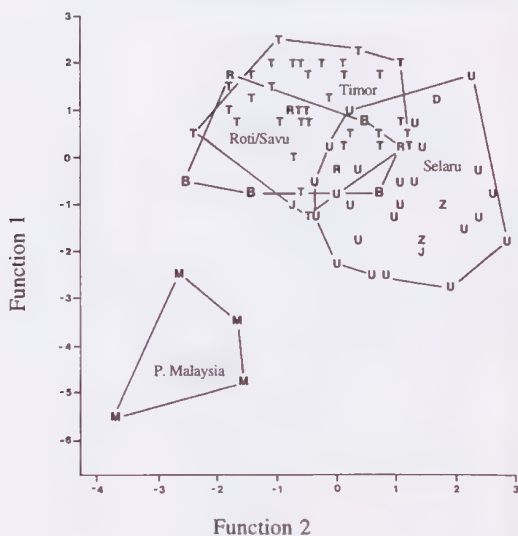


Figure 5 Plots of Functions 1 and 2 from Canonical Variate Analysis among four population groupings (Selaru, Timor, Roti/Savu and Peninsula Malaysia) - with the few Sumba, Sumbawa and Java specimens unallocated - and based on a subset of five external body characters. Population codes as for Figure 2.

referred to any of these Lesser Sunda subspecies. These two specimens agree in size with the measurements of a single specimen from Ruteng, Flores island reported in Hill and Rozendaal (1989). Further specimens will probably allow recognition of the Sumbawa and Flores form as a unique subspecies.

The following section formally recognises three new subspecies of *H. bicolor* in the Lesser Sunda islands.

SYSTEMATICS

Hipposideros bicolor tanimbarensis subsp. nov., Kitchener

Holotype

Western Australian Museum (WAM) No. M44287; adult female; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; collected by Ir. Ibnu Maryanto (Museum Zoologicum Bogoriense) and Ron Johnstone, Western Australian Museum), on 25 April 1993.

Type locality

Wesuri Cave, near Adaut, Selaru island, Tanimbar Island Group (8°09'S, 131°08'E); at sea level.

Paratypes (all from type locality)

12♀, 12♂; WAM (M43818, M44248-9,

M44252, M44254, M44259, M44261-8, M44271-2, M44275-6, M44279, M44281-3, M44286, M44290).

Diagnosis

Hipposideros bicolor tanimbarensis differs from *H. b. bicolor* [including also measurements from Hill (1983) and Tate (1941)] in averaging smaller in most cranial, dentary and dental measurements, except for tympanic bulla length and intercochlear distance. For example: absolutely smaller greatest skull length 17.2-18.0 (N = 18) *v.* 18.2-19.0 (3) and least interorbital breadth 2.5-2.7 (18) *v.* 2.9-3.0 (4). Posterior noseleaf breadth larger 5.1-5.9 (24) *v.* 4.7-4.9 (2). Interlachrymal distance narrower relative to dentary length (Figure 6). Dorsal pelage darker, tipped with Fuscous rather than Burnt Umber.

H. b. tanimbarensis differs from *H. b. atrox* in having a narrower: zygomatic width 8.8-9.3 (18) v. 9.5-9.7 (3); least interorbital breadth 2.5-2.7 (18) v. 2.8-2.9 (3); M³M³ width 5.5-6.0 (17) v. 6.1-6.4 (3). It has a longer digit 5 metacarpal length relative to forearm length (Figure 7); and narrower least interorbital breadth relative to dentary length (Figure 8). Glans penis distal end sharper and less rounded in craniocaudal view, and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broad and not bilobed; arms of distal bifurcation not as widely spaced or as broad (Figure 10). Dorsal pelage darker, tipped with Fuscous rather than Cinnamon.

H. b. tanimbarensis differs from *H. b. hilli* subsp. nov. in averaging larger in all characters, except least interorbital breadth, interlachrymal distance, cochlea length, and digit 5 metacarpal length.

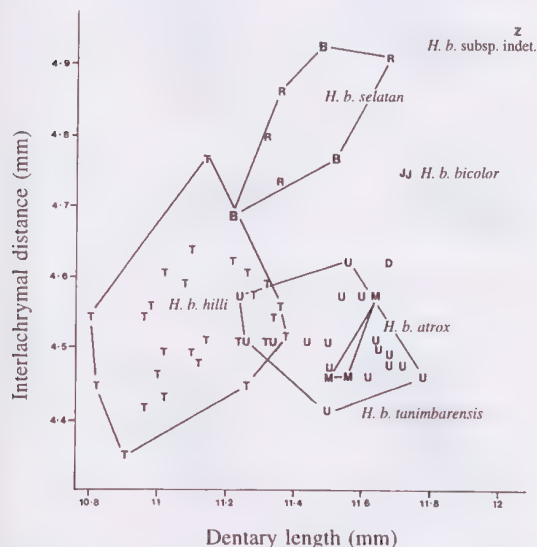


Figure 6 Plot of interlachrymal distance *versus* dentary length for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

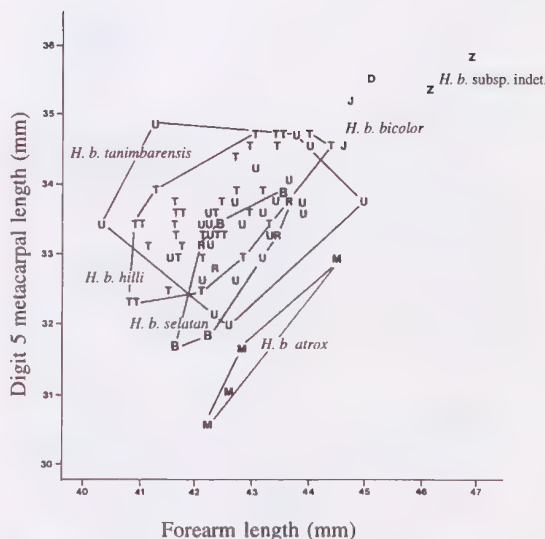


Figure 7 Plot of digit 5 metacarpal length *versus* forearm length for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

Dentary length shorter relative to least interorbital breadth (Figure 8). Dorsal pelage darker, tipped with Fuscous rather than Burnt Umber.

H. b. tanimbarensis differs from *H. b. selatan* subsp. nov. in having a narrower interlachrymal distance 4.4-4.6 (18) v. 4.7-4.9 (7) and narrower least interorbital breadth relative to dentary length (Figure 8). Dorsal pelage darker, tipped with fuscous rather than burnt umber.

Description

A moderate sized *H. bicolor* subspecies with greatest skull length 17.66 (17.16-17.98) 18 and forearm length 42.9 (40.3-45.0) 25. For other measurements see Table 2a, b. It agrees closely with the general description of the cranium, dentition and external body characters of this species as described by Hill (1963). *Hipposideros b. tanimbarensis* has zygomata broad, occasionally massive, with superior jugal projection low; zygomatic width narrower than mastoid width 9.08 (8.75-9.26) 18 *v.* 9.21 (9.03-9.41) 18; least interorbital breadth narrow 2.58 (2.45-2.71) 18; crown area of outer lower incisor slightly larger than that of inner lower incisors; anterior lower premolar three-quarters length and half to three-quarters height of posterior lower premolar; and vomer projection into mesopterygoid fossa only slightly thickened.

Pelage of ventral surface Smoke Gray; dorsal surface Smoke Gray base tipped with Fuscous. The patagia Dusky Brown.

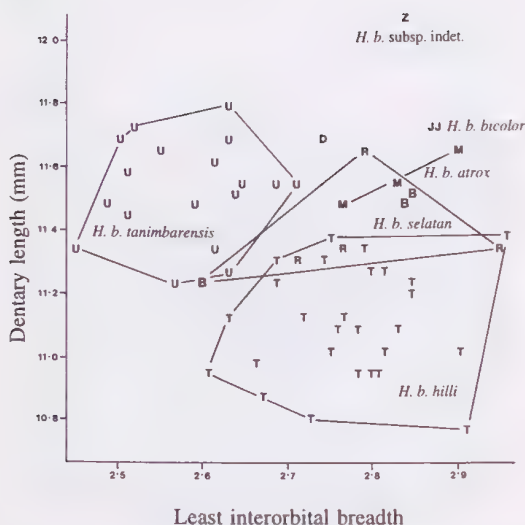


Figure 8 Plot of dentary length *versus* least interorbital breadth for populations of *Hipposideros bicolor*. Population codes as for Figure 2.

Penis ca. 7 mm long. Glans penis with distal head of variable shape; in craniocaudal view it ranges from a blunt rod shape (Figure 9b) to an arrow shape (Figure 9c) to a broadly rounded head with median distal slit (Figure 9d). Baculum ca. 3.0–3.2

mm long; base slightly broadened, long narrow shaft with short bifurcated distal tip (Figure 10b,c).

Distribution

Known only from the type of locality at Wesuri Cave, near Adaut, Selaru island, Tanimbar Group.

Etymology

Named after the Tanimbar Group of islands which it inhabits.

Referred Specimen

A single adult female (WAM M30345) mist netted over a river in a large limestone cave at Waikelosawah, Sumba island (9°36'S, 119°29'E) is tentatively referred to *H. b. tanimbarensis*; its measurements are presented in Tables 2a, b. On the basis of the more important cranial, dental and dentary measurements the DFA allocated it to *H. b. tanimbarensis*. Its glans penis is similar to Figure 9c; its baculum has a length of 2.74 mm and is similar to Figure 10b.

Hipposideros bicolor hilli subsp. nov. Kitchener

Holotype

Western Australian Museum (WAM) No. M34953; adult male; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate;

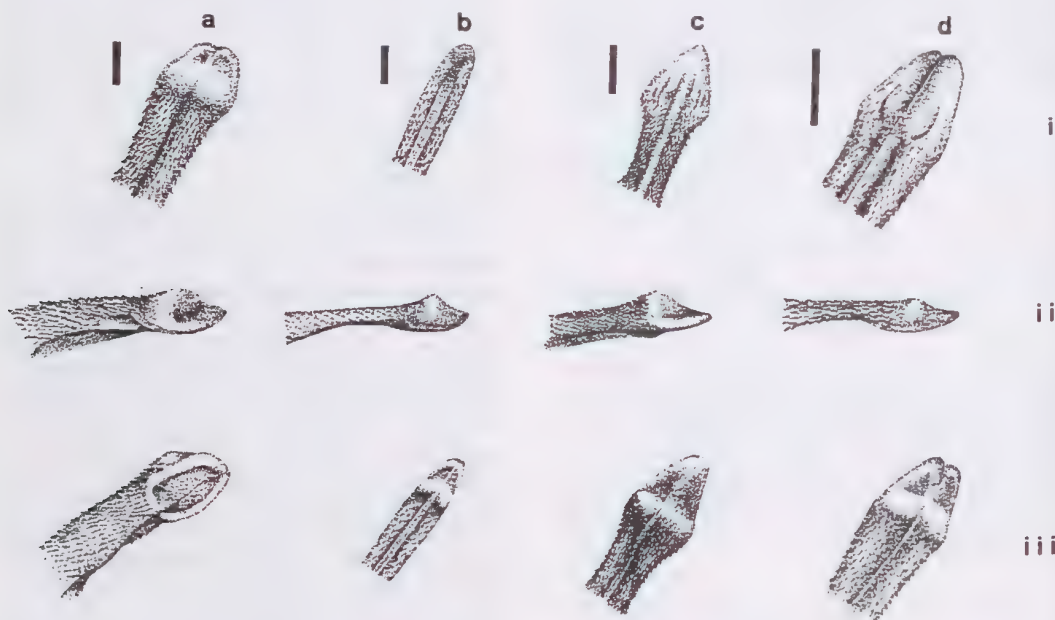


Figure 9 Glans penis of (a) *Hipposideros bicolor atrox* from Peninsula Malaysia (WAM M21159); (b) and (c) *H. b. selatan* subsp. nov. from Roti island (WAM M35375 and WAM M35507, respectively) and (d) *H. b. hilli* subsp. nov. from Timor island (WAM M34959). From (i) cranial, (ii) lateral and (iii) caudal views. Scale lines, 0.5 mm.

collected on 17 October 1990 by Dr Ken Aplin (Western Australian Museum) and Bapak Boeadri (Museum Zoologicum Bogoriense).

Type Locality

Mist netted in a cave at Oimoro, near Panite, West Timor, Nusa Tenggara Timur, Indonesia (9°50'S, 124°29'E); at sea level.

Paratypes

From the following localities on West Timor: Baumata (10°11'S, 123°43'E), 7♀, 5♂, WAM M(30060, 30098-9, 30107, 30110, 30115-6, 30118-22; Baurae (10°15'S, 123°43'E), 1♀, WAM M35010; Panite (9°50'S, 124°29'E), 11♀, 9♂, WAM M(34889-92, 34894, 34951-2, 34954-6, 34958-9, 34961, 34963-5, 34967-8, 34973-4).

Diagnosis

Hipposideros b. hilli differs from *H. b. bicolor* [including also Hill (1983) and Tate (1941) measurements] in averaging smaller in most measurements, except tympanic bulla length, M³ breadth, ear length and digit 5 metacarpal length. For example, absolute smaller in both greatest skull length 16.8-17.8 (27) *v.* 18.2-19.0 (3) and forearm length 40.8-44.4 (34) *v.* 44.6-46.8 (6). Dentary length relative to least interorbital breadth shorter (Figure 8).

Hipposideros b. hilli has similar cranial and external body measurements to *H. b. atrox* but differs in having considerably smaller dental measurements (see Table 2a). Dentary length relative to both interlacrimal distance and least interorbital breadth shorter (Figures 6 and 8, respectively). Digit 5 metacarpal length longer relative to forearm length (Figure 7). Glans penis distal end less rounded in craniocaudal view and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broadened and not bilobed, arms of the distal bifurcation not as widely spaced or as broad (Figure 10). Dorsal pelage darker, tipped with Burnt Umber rather than Cinnamon.

Hipposideros b. hilli differs from *H. b. tanimbarensis* as described in the earlier diagnosis of that subspecies.

Hipposideros b. hilli differs from *H. b. selatan* in averaging smaller in most cranial, dental and dentary characters. For example, greatest skull length 17.3 (16.8-17.8) 27 *v.* 17.6 (17.4-17.9) 7. Interlacrimal distance and dentary length generally smaller (Figure 6) and dentary length relative to least interorbital breadth generally smaller (Figure 8).

Description

Hipposideros b. hilli is on average, the smallest

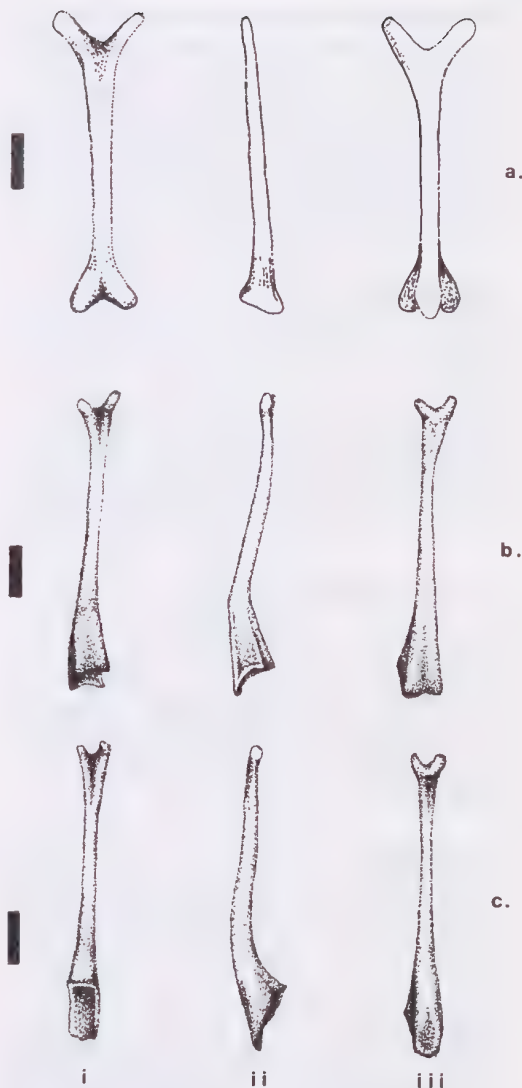


Figure 10 Baculum of (a) *Hipposideros bicolor atrox* from Peninsula Malaysia (WAM M21158), (b) *H. b. selatan* subsp. nov. from Roti island (WAM M35507), and (c), *H. b. hilli* subsp. nov. from Timor island WAM M34959). From (i) caudal, (ii) lateral and (iii) cranial views. Scale lines 0.5 mm.

form of *H. bicolor* in the Lesser Sunda Islands. It has a greatest skull length of 17.29 (16.82-17.78) 27 and forearm length of 42.3 (40.8-44.4) 34. Other measurements of cranium, dentition, dentary and external body characters (see Table 2a, b) are similar to *H. b. tanimbarensis*. Its zygomatic width is much narrower than the mastoid width 8.77 (8.49-8.96) 27 *v.* 9.10 (8.73-9.31) 27.

Pelage colour of the ventral surface Drab. The dorsum Drab tipped with Burnt Umber. Patagia Dusky Brown.

Penis *ca.* 7 mm long. Glans penis with distal head flattened craniocaudally and broadly rounded with a median terminal slit (Figure 9d). Baculum *ca.* 2.8 mm long, slightly broadened at base; shaft long, narrow, slightly flexed in lateral view with short bifurcated distal tip (Figure 10c).

Distribution

Several localities in West Timor (Baumata, Bauran and Panite), Nusa Tenggara Timur, Indonesia.

Etymology

Named after John Edwards Hill, formerly of the British Museum of Natural History. Although retired he continues to provide generous assistance to the new generations of chiropteran taxonomists.

Hipposideros bicolor selatan subsp. nov.

Kitchener

Holotype

Western Australian Museum (WAM) No. M 35421; adult female; 'scientific' skin; carcass fixed in 10% formalin and preserved in 70% ethanol; skull separate; collected on 9 October 1990 by D.J. Kitchener.

Type locality

Desa Sanggoen, 6 km SW Baa, Roti island, Nusa Tenggara Timur, Indonesia (10°43'S, 123°09'E); collected by hand in a small limestone cave; at sea level.

Paratypes

From Roti island: Kota Baa (10°44'S, 123°06'E), 1♂, WAM M35375; Desa Oeseli (10°51'S, 123°05'E), 2♀, WAM M35506-7. From Savu island: Desa Menia (10°29'S, 121°55'E), 1♀, 3♂♂, WAM M(35115, 35119, 35130, 35211).

Diagnosis

Hipposideros b. selatan differs from *H. b. bicolor* [including also measurements from Hill (1983) and Tate (1941)] in averaging smaller in most cranial measurements, except tympanic bulla length, interlachrymal distance and cochlea length, all dental measurements and most external measurements except noseleaf breadth and ear length (see Table 2a). For example, greatest skull length 17.4-17.9 (7) *v.* 18.2-19.0 (3); digit 3 metacarpal length 30.4-33.0 (8) *v.* 34.3-34.4 (2); and forearm length 41.6-43.7 (8) *v.* 44.6-46.8 (6). Posterior noseleaf breadth larger 5.4-6.5 (8) *v.* 4.7-4.9 (2).

Hipposideros b. selatan is similar in overall size to *H. b. atrox* (see Table 2a, b). It differs in having a smaller: zygomatic width 8.9-9.2 (7) *v.* 9.5-9.7 (3) and M³M³ width 5.6-6.0 (7) *v.* 6.1-6.4 (3) and larger interlachrymal distance 4.7-4.9 (7) *v.* 4.5-4.6 (3). Interlachrymal distance relative to dentary length larger (Figure 6). Glans penis distal end less rounded in craniocaudal view and from lateral view distal tip longer (Figure 9). Baculum more gracile, base not as broadened and not bilobed, arms of distal bifurcation not as widely spaced or as broad (Figure 10) Dorsal pelage darker, tipped with Burnt Umber rather than Cinnamon.

Hipposideros b. selatan differs from both *H. b. tanimbarensis* and *H. b. hilli* as described in the earlier diagnoses of these two subspecies.

Description

Approximately the same overall size as *H. b. tanimbarensis* with which it agrees in general form of cranium (apart from differences noted in the earlier diagnosis), dentition and dentary (see Table 2a, b). Greatest skull length 17.59 (17.35-17.85) 17 and forearm length 42.7 (41.6-43.7) 8. Zygomatic width narrower than mastoid width 9.00 (8.85-9.15) 7 *v.* 9.15 (8.98-9.30) 7.

Pelage colour of ventral surface Drab. The dorsum Drab tipped with Burnt Umber. Patagia Dusky Brown.

Penis *ca.* 5 mm long, glans shape variable, with forms ranging from those shown in Figure 9 b, c and d. Baculum *ca.* 3.2 mm long, with shaft long, bifurcated slightly at distal tip (Figure 10b) but also with bifurcate arms closer together.

Distribution

Roti and Savu islands, Nusa Tenggara Timur, Indonesia.

Etymology

The most southern populations of *H. bicolor*. Selatan is Bahasa Indonesian for southern.

DISCUSSION

Hipposideros bicolor is a widespread Asian species that prior to this study was known to be distributed from mainland Asia (northern India through Assam, Burma, southern China, Thailand, Vietnam, Malay Peninsula) to the southeast islands of Sumatra, Java, to Flores island in the Lesser Sunda Islands, Sulawesi and Philippines and several smaller associated islands. This study confirms that it also extends eastwards along the southern chain of Indonesian islands as far as the Tanimbar Group. In this southern chain of islands it differentiates morphologically into three subspecies which have a stronger phenetic relationship with *H. b. bicolor* of Java rather than

with *H. b. atrox* of Peninsula Malaysia. It may be that the form of *H. bicolor* on Sumbawa island is a further subspecies.

The morphological differentiation of a number of species of micro- and megachiroptera into two or three subspecies in the Lesser Sunda islands has been documented (Kitchener and Suyanto 1996). This morphological differentiation shows some patterns, and as summarised by Kitchener and Suyanto (1996), "reflect the last major glacial (18,000 yr BP) island arrangement (and) suggests that many of these morphological changes, presumably reflecting evolutionary processes, are of relatively recent origin". These authors further state that such differentiation to subspecies tends to occur in the easternmost islands or on islands in the Outer Banda Arc (Sumba, Roti, Savu and Timor). *Hipposideros bicolor* has followed these general patterns and differentiated into subspecies on the easternmost island of Selaru and on islands in the Outer Banda Arc (Timor and Roti/Savu). Interestingly, the single specimen from the island of Sumba in the Outer Banda Arc, appeared to be phenetically closer to the population of *H. bicolor* on Selaru island than to the populations on the isolated islands in the Outer Banda Arc of Roti/Savu and Timor.

Only two studies have examined the association between geographic variables and morphology among bats in the region (Kitchener *et al.* 1992, Kitchener and Maharadatunkamsi 1996). These studies showed that longitude was the most important associate in determining overall skull and body size. In the former study, *Hipposideros diadema* tended to be smaller towards the east contrasting with the latter study on *Cynopterus nusatenggara* which tended to be larger to the east. *Cynopterus nusatenggara* also became larger on more isolated islands. The form of *H. bicolor* on the western island of Sumbawa was much larger than those forms on islands to the east and south - suggesting that this species followed the overall size trend of its congener.

Other specimens examined

Hipposideros bicolor bicolor

Kiskenda, Java (7°06'S, 110°16'E); 2♀♀; WAM M(39314, 39360).

Hipposideros bicolor atrox

Ampang Impounding, Selangor Peninsula Malaysia (3°08'N, 101°46'E); 2♀♀, 2♂♂; WAM M(21158-61).

ACKNOWLEDGEMENTS

We gratefully acknowledge the support of the

Executive Director, Western Australian Museum, Mr Andrew Reeves; the Director, Puslitbang Biologi (LIPI), Dr Soetikno Wirjoatmodjo, and the Director, Balitbang Zoologi (LIPI), Drs M. Amir.

To our many colleagues who assisted greatly in the field, particularly Dr R.A. How and Mr R. Johnstone, Western Australian Museum; Ir I. Maryanto, Ir Maharadatunkamsi and Bapak Boedi, Balitbang Zoologi, we extend our thanks for their efforts and companionship.

Expedition costs were defrayed by grants to D. Kitchener from: National Geographic Society, Washington and Australian Nature Conservation Agency, Canberra. Some expenses were borne personally. Garuda Indonesia kindly defrayed freight costs of the expeditions. Mrs N. Cooper, Western Australian Museum, ran the computer analyses. Mrs S. Dalton, Western Australian Museum, typed the manuscript.

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Manuscript received 3 May 1996; accepted 27 September 1996.

Plio–Pleistocene *Peronella* (Echinoidea: Clypeasteroidea) from Western Australia

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Abstract – Three species of the laganid clypeasteroid *Peronella* are described from sediments of Pliocene and Pleistocene age in the Carnarvon, Perth and Eucla Basins in Western Australia. The oldest is *Peronella ova* sp. nov. from the Pliocene Roe Calcarene of the Eucla Basin. *Laganum decagonale rictum* Gregory, 1892, is redescribed, elevated to specific status and placed in the genus *Peronella*. *Peronella ricta* appears to be restricted to the basal part of the Carbla Oolite, a Middle Pleistocene formation in the Carnarvon Basin outcropping around Shark Bay. Late Pleistocene sediments in the Shark Bay region contain the still extant species *P. orbicularis*. The living species *P. lesueuri* is recorded from Holocene sediments in the Perth Basin. A key to fossil *Peronella* in Western Australia permits differentiation of the four known species by reference to test length, test thickness and petal length. The genus is of only limited biostratigraphical utility in the late Cenozoic of this region.

INTRODUCTION

In 1892 the first fossil echinoid was described and figured from the western half of Australia by J.W. Gregory of the British Museum (Natural History) in London. The specimen, described by Gregory (1892: 433–435) as "*Laganum decagonale*, Lesson. Var. *rictum*, n.var." had been sent by the Western Australian Government Geologist from 1888–1895, Harry Page Woodward (McNamara and Dodds 1986), to Gregory in London, where it was deposited in the British Museum (Natural History) and given the catalogue number E3770. According to Gregory the specimen was from the "Cainozoic of Shark's [sic] Bay, West Australia". Another specimen from the same locality was retained by Woodward and placed in his collection (No.81; WAM 96.208), now housed in the palaeontology collections in the Western Australian Museum.

Since being described, this form has variously been either raised to specific status (e.g., Clark 1946) or synonymised with other living species, notably a living species, *Peronella lesueuri* (e.g., Mortensen 1948: 271; Logan *et al.* 1970: 56). Clark (1946) recognised that this form belonged in *Peronella* rather than *Laganum*, on the basis of the presence of four, not five, gonopores. However, he observed that "*ricta* . . . must be considered [a] *Peronella* whose specific limits and geographical distribution are not satisfactorily known". Mortensen (1948), on the contrary, considered the Shark Bay form to be very closely related to *Peronella lesueuri*, and "possibly identical with it".

In their study of the history of carbonate sedimentation in Shark Bay, Logan *et al.* (1970) identified it unequivocally as *Peronella lesueuri* [sic]. These actions were all taken on the basis of Gregory's description and line drawing of the specimen, not on the basis of extra material.

Fieldwork in the Shark Bay region in the 1980s by the author has resulted in the collection of 103 specimens of this echinoid, enabling its specific status to be firmly established. Furthermore, another species, *Peronella orbicularis*, also occurs in the extensive Pleistocene deposits that outcrop in this region (see Kendrick *et al.* 1991). These two species from different Pleistocene units are described herein in detail for the first time.

Pliocene occurrences of *Peronella* in Western Australia are restricted to the Roe Calcarene, which outcrops on the Roe Plains in the Eucla Basin (Figure 1). Foster and Philip (1980) placed this species in the extant *Peronella orbicularis*. However, the Pliocene species has a number of characteristics that clearly distinguish it from the living species. It is herein described as a new species. These Plio–Pleistocene species, including true *P. orbicularis*, are described and their stratigraphic distribution, and that of a Holocene species of *Peronella*, discussed.

BIOSTRATIGRAPHY

All of the material of Gregory's "*Laganum decagonale*, Lesson. Var. *rictum*, n.var." was collected from the Gladstone Embayment, on the

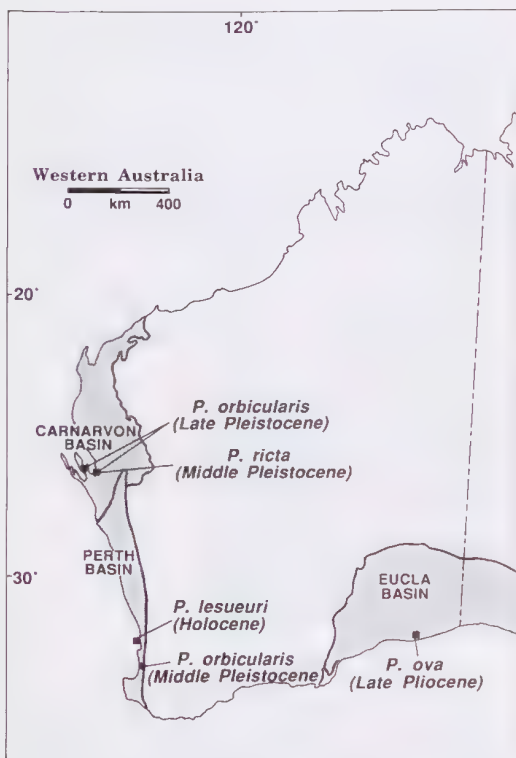


Figure 1 Map showing the locations of fossil *Peronella* in the Carnarvon, Perth and Eucla Basins, Western Australia.

southeastern arm of Shark Bay, immediately north of Hamelin Pool and the Faure Sill (Figure 1). The bed containing the echinoids is a fossiliferous limestone, less than one metre in thickness, that outcrops at Wooramel Cliff, Gladstone Bluff, Gladstone Jetty and in gullies along the Toolonga Scarp (Logan *et al.* 1970). The specimens used in this study were collected from approximately 2 km south of Gladstone Jetty to about 100 m north of the Jetty, from outcrops of limestone that occur in the intertidal zone, 200–300 m seaward of high water mark.

This limestone was termed the "Gladstone unit" by Davies (1970), and was regarded by Logan *et al.* (1970) as being laterally equivalent to the basal beds of the Carbla Oolite. Playford *et al.* (1975) called this unit the Gladstone Member of the Carbla Oolite. This classification is followed herein. The Carbla Oolite was provisionally considered by Kendrick *et al.* (1991) as being correlated with Oxygen Isotope Stage 7 (220,000 – 235,000 BP) of the Middle Pleistocene.

In addition to the presence of the species of *Peronella*, this unit has yielded the spatangoid echinoid *Breynia desorii* (Gray), a species which is still living in Shark Bay today (McNamara 1982). In

addition, there is a molluscan fauna that includes *Pecten modestus* Reeve, *Dendostrea folium* (Linnaeus), *Fragum* (*Lunulicardia*) sp., *Circe* sp., *Tagelus* sp., *Clementia papyracea* (Gray), *Dosinia* (*Pectunculus*) cf. *sculpta* (Hanley), and *Strombus* (*Doxander*) *campbelli* Griffith and Pidgeon (specimens WAM 87.528 to 87.535, identified by G.W. Kendrick). The foraminifer *Marginopora vertebralis* Blainville is also a common element, indicating, as Logan *et al.* (1970) suggested, that this "Peronella assemblage" occupied open sandy patches in seagrass meadows.

Overlying the Gladstone Member in the eastern part of Shark Bay is a unit of shelly calcarenite, containing well-preserved aragonitic shell, which is probably equivalent to the Dampier Formation. A small species of *Peronella*, attributable to the living species *P. orbicularis*, occurs in this unit. The same species has been recovered from the Dampier Formation on the Peron Peninsula. Rarely more than 1 m in thickness, the Dampier Formation is a bivalve-rich limestone and lithoclast grainstone. While this formation was considered by Logan *et al.* (1970) to be of Middle Pleistocene age, Uranium-series dates from the coral *Goniastrea* (Kendrick *et al.* 1991) indicate a Late Pleistocene, Last Interglacial, age for this formation.

The oldest species of *Peronella* to occur in Western Australia is found in the Eucla Basin in the Roe Calcarenite. While Foster and Philip (1980) followed Ludbrook (1978) in ascribing a Pleistocene age to this richly fossiliferous unit, Kendrick *et al.* (1991) favoured a Late Pliocene age, on the basis of the nature of the molluscan fauna. Unfortunately, the echinoid fauna, as described by Foster and Philip (1980), provides no corroborating evidence one way or the other. In addition to *Peronella*, Foster and Philip (1980) recorded *Microcyphus annulatus* Mortensen, *Amblyneustes formosus* Valenciennes and *Amblyneustes* sp. nov.

Specimens referred to in this study are housed in the invertebrate palaeontology collections of the Western Australian Museum (WAM) and the Natural History Museum, London (BMNH). Measurements were made with an electronic calliper to an accuracy of 0.01 mm. A number of parameters are expressed as percentages of test length (%TL).

SYSTEMATIC PALAEOLOGY

Order Clypeasteroida A. Agassiz, 1872

Family Laganidae A. Agassiz, 1872

Genus *Peronella* Gray, 1855

Type species

Laganum peronii L. Agassiz, 1841: 123; by original designation

Key to fossil species of *Peronella* from Western Australia

- 1. Test large, reaching more than 50 mm in length 2
Test small, reaching less than 50 mm in length 3
- 2. Test thin, with petals open distally .. *P. lesueurii*
Test thick, with petals closed distally *P. ricta*
- 3. Petals extending about two-thirds of the distance to ambitus *P. ova*
Petals extending about one-half of the distance to ambitus *P. orbicularis*

Peronella ova sp. nov.
Figure 2

Peronella orbicularis (Leske, 1778): Foster and Philip 1980: 156.
Peronella platymodes (Tate, 1893): Kendrick 1985: figure 3C.
Peronella sp.: McNamara 1988: 158, figure 12.5

Material Examined

Holotype
WAM 94.854 from the Late Pliocene Roe

Calcarenites, Roe Plains, Madura district, Western Australia; pit 0.5 km north of Hampton Microwave Repeater Tower. Collected by V.A. Ryland and G.W. Kendrick, 1980.

Paratypes
All from the Roe Calcarenites: WAM 82.2103–82.2121, 82.2255, 82.2273–2283, 94.853, 94.855, 94.856 from same locality and horizon as the holotype; WAM 82.2095–6, spoil heaps at base of Hampton Microwave Repeater Station; WAM 82.2135–2143, 82.2241–2248, 94.850, 94.848, 94.849, 94.851, 94.852, 94.854, pit 1.5 km north of Hampton Microwave Repeater Station; WAM 85.2025, 89.754, pit 2.5 km north of Hampton Microwave Repeater Station; WAM 82.2151 (4 specimens) from doline of Nurina Cave N.46, about 5.5 km southwest of Madura Cave; 85.1876 (3 specimens) from Main Roads Department quarry, 16 km south of Madura Roadhouse.

Etymology
From the Latin *ovum*, egg, alluding to the occurrence of the species in the Roe Calcarenites, and to the ovate outline of the test.

Diagnosis
Test low, thick; petals relatively long, extending about two-thirds of the way to ambitus. Peristome

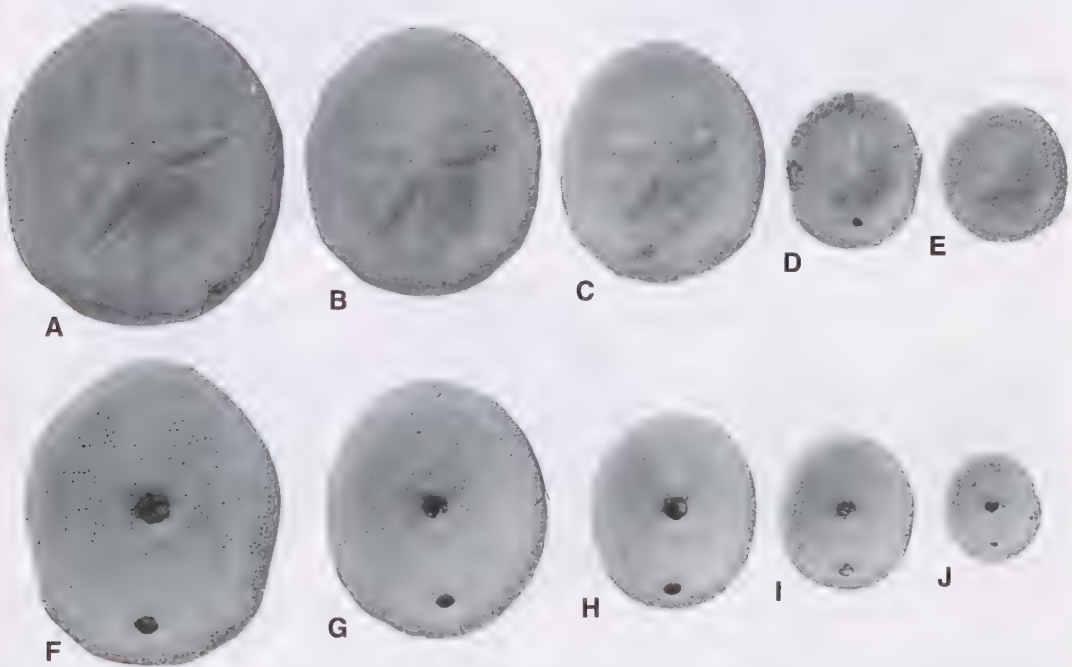


Figure 2 *Peronella ova* sp. nov. from the Late Pliocene Roe Calcarenites, Roe Plains, Western Australia; A, WAM 82.2096; B, WAM 82.2105; C, WAM 82.2113; D, WAM 82.2280; E, WAM 94.853; F, WAM 94.854, holotype; G, WAM 82.2118; H, WAM 82.2163; I, WAM 82.2120; J, WAM 94.849; all x1.5, except E, which is x4.

large; food grooves short and weakly developed, extending less than a quarter the distance from the peristome to the ambitus. Periproct situated less than twice its diameter from posterior margin, except in very large specimens.

Description

Test small, reaching up to 44 mm test length (TL); ovate, with a thick, broadly rounded ambitus; posterior margin (interambulacrum 5) transverse; margins of ambulacra I and II and interambulacra 1 and 4 also straight, intersecting each other with sharp angle; margin anterior of interambulacra 1 and 4 broadly rounded. Test low, being highest at mid-test length at apical system; height 13–22%TL; rarely, in large specimens, as narrow as 77%TL; juveniles almost flat with relatively thinner margin; at margin test height varies between 10–20%; test longer than wide, width ranging between 84–92%TL; wider in small individuals, narrowing with increase in test size. Aboral surface rises slightly from lateral margin. Apical system slightly anterior of centre; tuberculate, with four gonopores. Petals closed or almost closed distally (Figure 2A). Decrease in relative width during ontogeny. Paired petals of equal length (17–26%TL), but slightly shorter than anterior petal in ambulacrum III (23–32%TL); extend about two-thirds of the way to the ambitus; maximum width varying between 10–17%TL; relatively broad in juveniles (Figure 2E), narrowing slightly during ontogeny; petals widest at about mid-petal length. Interporiferous region 6–11%TL, being widest in smallest specimens (Figure 2E). Inner pores of each pair circular; outer pore elongate; connected by shallow interporiferous furrow.

Adoral surface concave, sloping at low angle to sunken peristome. Peristome circular, large, diameter 8–13%TL; central or slightly anterior of centre; bourrelets absent. Food grooves very short and weakly developed, extending less than a quarter of the distance from the peristome to the ambitus in the largest specimens (Figure 2F). Periproct circular to transversely oval; 4–7%TL in width; smaller than peristome and usually situated less than twice its length from the posterior border. However, in two very large specimens (WAM 82.2095 and 85.2025, TL 43.2 mm and 44.7 mm, respectively) periproct situated greater than twice the periproct diameter from posterior ambitus.

Discussion

The Late Pliocene *Peronella ova* can be distinguished from the Late Pleistocene to Recent *P. orbicularis* by its relatively narrower, lower test with thicker margins; longer petals; larger peristome; weaker, shorter food grooves; and periproct situated closer to the posterior ambitus (except in very large specimens). It differs from

another living Western Australian species, *P. tuberculata* Mortensen, 1918, from northwestern Australia, in possessing a relatively narrower test; periproct situated closer to the posterior margin; shorter food grooves; and flatter adoral surface. *P. ova* differs from the Middle Pleistocene *P. ricta* in possessing a lower test with thicker margins; relatively broader, longer petals; more concave adoral surface with slightly larger peristome and weaker, shorter food grooves.

The other Australian Pliocene species of *Peronella* is *P. platymodes* (Tate, 1893) from the Late Pliocene Hallett Cove Sandstone. This species has a much thinner, narrower test than *P. ova*, combined with appreciably shorter petals. Of the four Pliocene species of *Peronella* described from Okinawa by Cooke (1954), *P. ova* most closely resembles *P. kamimura* Cooke, 1954. However, the Australian species can be distinguished by its longer petals that are closed distally and periproct situated closer to the posterior margin.

Peronella ricta (Gregory, 1892)

Figures 3, 4

Laganum decagonale rictum Gregory 1892: 435–437, Pl.12, figures 1a–c; Mortensen 1948: 271.

Peronella ricta: Clark 1946: 34.

Peronella lesueri (sic.): Logan *et al.* 1970: 56, 62, 73, figures 10–5, 16–7.

Peronella rictum: McNamara 1988: 158, figure 12.5.

Material Examined

Holotype

BMNH E3770 (Gregory 1892, figures 1a–c) from the "Cainozoic. Shark's Bay, West Australia".

Other material

WAM 1808; 11027; 66.805; 78.352–78.354; 81.610 (3); 83.771–83.782, 83.799 – 83.815; 87.545 (66 specimens); 89.409 (five specimens); 96.208; 96.209 from the Gladstone Member of the Carbla Oolite (Middle Pleistocene), approximately 2 km south of Gladstone Jetty to about 100 m north of the Jetty, from outcrops of limestone that occur in the intertidal zone, 200–300 m seaward of high water mark.

Diagnosis

Moderately large species of *Peronella* with relatively narrow, thick test; relatively narrow petals that are distally closed and extend just over half way to ambitus. Adoral surface of test almost flat. Food grooves short but moderately sunken proximally. Periproct less than twice its diameter from posterior margin.

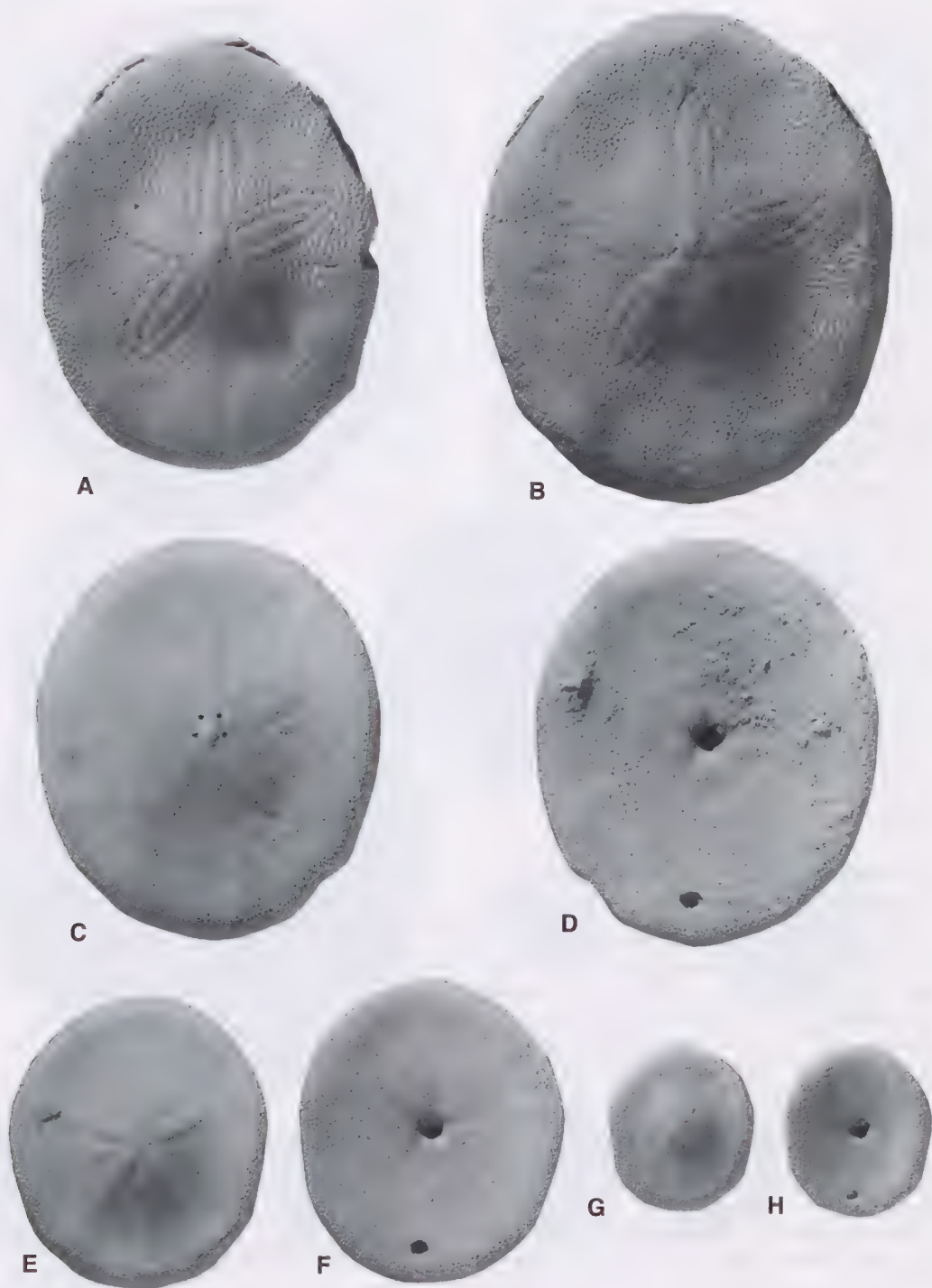


Figure 3 *Peronella ricta* (Gregory, 1892) from the Middle Pleistocene Gladstone Member of the Carbla Oolite, near Gladstone Jetty, Shark Bay, Western Australia: A, WAM 96.208; B, WAM 1808; C, D, WAM 83.806; E, F, WAM 83.788; G, H, WAM 96.209; all x1.5.

Description

Test moderately large, reaching up to 86 mm test length (TL); ovate, with a broadly rounded ambitus; posterior sometimes broadly acuminate; highest at mid test length at apical system; height 15–23%TL; juveniles almost flat; at margin test height varies between 8–20%, being higher in small individuals; test longer than wide, width ranging between 78–94%TL; widest in small individuals (Figure 3G,H), narrowing with increase in test size. Aboral surface rises gently from lateral margin, increasing angle of slope up to apex. Apical system slightly anterior of centre; tuberculate, with four gonopores. Petals closed or almost closed distally. Increase in relative length during ontogeny. Paired petals of equal length (18–28%TL), but slightly shorter than anterior petal in ambulacrum III (23–34%TL); extend just over half way to the ambitus (Figure 3B,C,E); petals narrow, with maximum width varying between 7–15%TL; relatively broad in juveniles (Figure 3G), narrowing relatively during ontogeny; petals widest at about mid-petal length. Interporiferous region 4–8%TL, being widest in smallest specimens. Inner pores of each pair circular; outer pore elongate; connected by shallow interporiferous furrow.

Adoral surface flat, sloping at very low angle to slightly sunken peristome. Peristome circular and surrounded by weakly developed bourrelets (Figure 3D); central or slightly anterior of centre. Food grooves short, but relatively deeply sunken close to peristome (Figure 4B). Periproct circular to transversely oval; similar in size to peristome and situated less than twice its diameter from the posterior border (4–11%TL).

Discussion

Peronella ricta can be distinguished from the living *P. lesueuri* in a number of ways. Although being a relatively large species of *Peronella*, *P. ricta* does not attain as large a test size. The test of *P. ricta* is much thicker, *P. lesueuri* being a particularly thin species of *Peronella*. At comparable test sizes, the petals of *P. ricta* are longer. Furthermore, they are virtually closed distally, whereas those of *P. lesueuri* are open. The interporiferous zone of the petals in *P. lesueuri* is slightly more swollen than in *P. ricta*. On the adoral surface, the food grooves are much deeper close to the peristome in *P. ricta*, resulting in the presence of more pronounced bourrelets.

The other species of *Peronella* that occurs in the Shark Bay region today, and did so in the Late Pleistocene, is *P. orbicularis*. *P. ricta* can be distinguished by its larger size; relatively narrower test that is more rounded posteriorly; more evenly sloping aboral surface; relatively longer, narrower petals; flatter adoral surface; periproct set closer to the posterior ambitus, less than two periproct

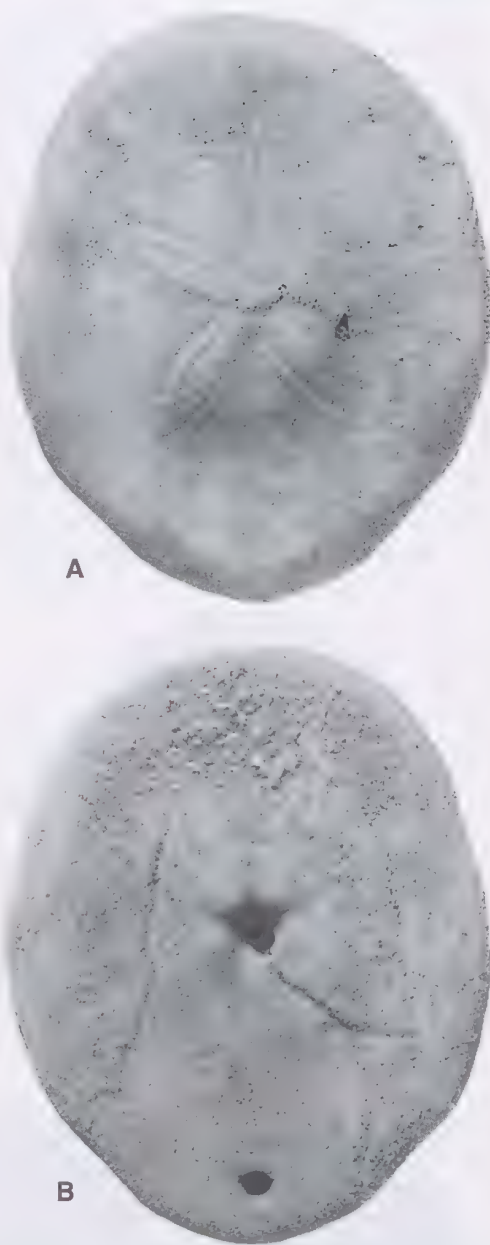


Figure 4 *Peronella ricta* (Gregory, 1892) from the Middle Pleistocene Gladstone Member of the Carbla Oolite, near Gladstone Jetty, Shark Bay, Western Australia: WAM 83.782, A, aboral view of teratological specimen with only four petals; B, adoral view of same specimen; both $\times 1.5$.

diameter widths away, whereas in *P. orbicularis* it is at least two periproct widths away. The test of *P. ricta* is relatively narrower than that of the third living Western Australian species, *P. tuberculata*. Furthermore, it has narrower petals; flatter adoral

surface; periproct situated closer to the posterior margin and shorter food grooves.

Teratological specimens of *P. ricta* are rare, but one is known (WAM 83.782) in which ambulacrum II is not developed on the aboral surface, hence only four petals are present (Figure 4A). On the adoral surface, however, ambulacrum II is present, the specimen possessing the normal complement of five food grooves (Figure 4B).

Peronella orbicularis (Leske, 1778)
Figure 5

Echinodiscus orbicularis Leske, 1778: 208, Pl.45, figs 6,7.

Peronella orbicularis: Mortensen 1948: 286–291; Pl. 51, figs 1–18 (with full synonymy); McNamara 1988: 158, figure 12.5.

non *Peronella orbicularis*: Foster and Philip 1980:156.

Material Examined

WAM 87.610 (157 specimens); WAM 96.210–96.218 (nine specimens) from the Bibra Formation (Late Pleistocene), Yaringa Station, Shark Bay, Western Australia, from large claypan 400 m west of northwest coastal highway; WAM 93.252 (six specimens) from the Dampier Formation (Late Pleistocene), Peron Peninsula, Shark Bay, from southern end of “Big Lagoon”, on east side, 1 m thick shell bed that is 1 m above high water mark; four specimens (WAM 94.266) from a Middle Pleistocene unit at Dumbarton, near Busselton in the Perth Basin.

Emended Diagnosis

Small species of *Peronella* with circular test with thickened rim; relatively broad petals that are distally closed and rarely extend more than half way to ambitus. Adoral surface of test slightly

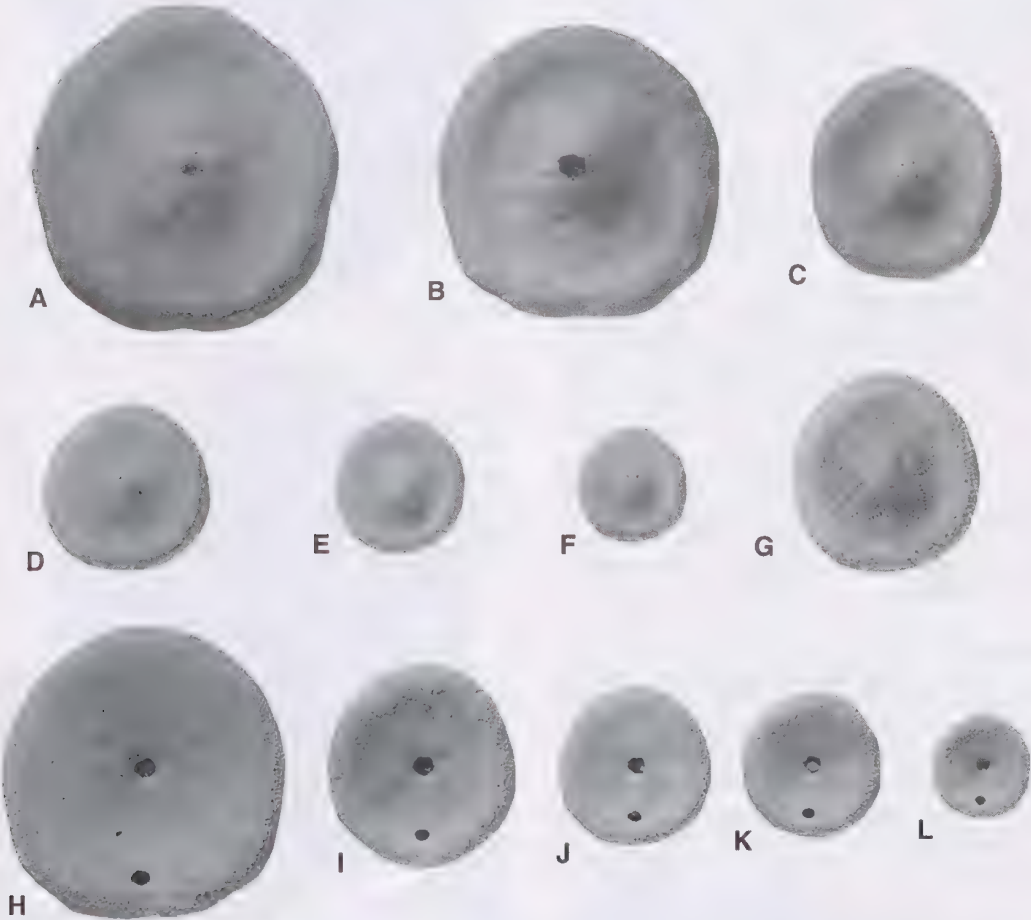


Figure 5 *Peronella orbicularis* (Leske, 1778) from the Late Pleistocene Dampier Formation, Shark Bay, Western Australia: A, H, WAM 93.252c; B, WAM 93.252d; C, WAM 96.211; D, WAM 96.213; E, WAM 96.212; F, WAM 96.214; G, WAM 96.210; I, WAM 96.215; J, WAM 96.216; K, WAM 96.217; L, WAM 96.218; all x1.5, except G which is x4.

concave; peristome a little sunken. Food grooves relatively long, extending about one-third of the way to the ambitus in larger specimens. Peristome and periproct small. Periproct situated at least two periproct diameters from posterior margin.

Description

Test small, reaching up to 35 mm test length (TL); subcircular, with a broadly rounded ambitus; posterior generally truncate (Figure 5A,B,H); highest at mid-test length at apical system; height 19–26%TL; large adults relatively lower than smaller adults; at margin test height varies between 12–20%, being higher in small individuals; test slightly longer than wide, width ranging between 91–99%TL. Aboral surface rises gently and evenly from broadly rounded lateral margin up to apex. Apical system slightly anterior of centre; tuberculate, with four gonopores. Petals almost closed or slightly open distally. Paired petals of equal length (17–24%TL, but slightly shorter than anterior petal in ambulacrum III (20–28%TL); extend about half of the way to the ambitus; petals broad, with maximum width varying between 10–16%TL; relatively broad in juveniles (Figure 5G), narrowing slightly during ontogeny; petals widest at about mid-petal length. Interporiferous region 6–10%TL, being widest in smallest specimens. Inner pores of each pair circular; outer pore slightly elongate; connected by shallow interporiferous furrow.

Adoral surface gently concave, sloping at low angle to slightly sunken peristome. Peristome small in adults, 6–10%TL; larger in juveniles, up to 18%TL in specimen of 8 mm TL; circular and surrounded by weakly developed bourrelets; central or slightly anterior of centre. Food grooves of moderate length and well-impressed (Figure 5H,I), extending about one-third of the way to the ambitus. Periproct circular to transversely oval, with a width similar to peristome diameter; situated at least twice its length from the posterior border (9–15%TL).

Discussion

The living *Peronella orbicularis* occurs in the shallow intertidal zone in Western Australian waters from the far north of the state at a latitude of 14°S, south to Shark Bay at a latitude of 26°S. It extends further south only offshore, reaching to 31°34'S, some tens of kilometres off Guilderton. Although Rowe and Gates (1995) give its bathymetric range as 0–70 m, it has been collected off Guilderton in water depths of 106–110 m, 40 km west of Jurien Bay (latitude 30°21'S) at 165 m, and off Green Head (latitude 30°S) from between 190 and 238 m. Its presence offshore this far south, but absence inshore, can be attributed to southerly dispersal in the offshore Leeuwin Current (see

McNamara 1992 for a discussion of the effect of this current on the southerly dispersal of echinoids). It occurs in Late Pleistocene deposits in the Shark Bay region, but is absent from coeval deposits in the Perth Basin. However, four specimens from a Middle Pleistocene unit at Dumbarton, near Busselton in the Perth Basin (WAM 94.266), although poorly preserved, probably belong to this species, having, like *P. orbicularis*, a relatively broad test, relatively short petals and periproct that is not less than two diameters from the posterior ambitus.

The living species occupies a range of habitats, specimens in the collections of the Western Australian Museum recording its presence from intertidal reef flats to at least 200 m. It inhabits a variety of substrates, from coarse gravel to sand, muddy sand to silt. In shallow water it is found in association with mangroves or seagrass, but with coralline algae nodules and bryozoa in deeper water off the coast.

Peronella orbicularis can be distinguished from another living northwest Australian species, *P. tuberculata*, in having shorter petals and periproct situated closer to the posterior margin.

PLIOCENE TO HOLOCENE DISTRIBUTION OF PERONELLA IN WESTERN AUSTRALIA

Peronella is today a Tropical Indo-West Pacific genus, having been recorded from near-shore environments around Australia, Japan, Taiwan, Malaysia, Philippines, Polynesia and Indonesia (Mortensen 1948). Seven species are known from Australian waters (Rowe and Gates 1995). The stratigraphic distribution of *Peronella* is essentially from the Pliocene to the Recent. Species recorded as *Peronella* from the Eocene of Trinidad, Cuba and the southeastern United States (Cooke 1942) are now placed in *Weisbordella*, a neolaganid (Durham 1954). Pliocene species have previously been described from Japan (Cooke 1954), the Philippines (Israelsky 1933) and South Australia (Tate 1893).

	Eucla Basin	Perth Basin	Carnarvon Basin
Hol.		<i>P. lesueurii</i>	<i>P. lesueurii</i>
Late Pleis.			<i>P. orbicularis</i>
Mid. Pleis.		<i>P. orbicularis</i> ?	<i>P. ricta</i>
E. Pleis.			
Late Plio.	<i>P. ova</i>	<i>P. sp. indet.</i>	

Figure 6 Biostratigraphical distribution of fossil species of *Peronella* in the Eucla, Perth and Carnarvon Basins in Western Australia.

Species of *Peronella* are of limited biostratigraphical value in the western part of the continent (Figure 6). The Middle Pleistocene *P. ricta* has only been recognised with certainty from a very restricted area of Shark Bay. Four poorly preserved specimens of *Peronella* from the Middle Pleistocene of the Perth Basin near Busselton, appear much closer to *P. orbicularis* than they do to *P. ricta*. In the Carnarvon Basin *P. orbicularis* is restricted to the Late Pleistocene and Holocene. As

such, species of *Peronella* have some biostratigraphical utility in the Carnarvon Basin, allowing Middle and Late Pleistocene units to be characterised. The well-known living *P. lesueuri* appears to be restricted to the Holocene in the Perth and Carnarvon Basins. This species is morphologically quite distinct from the other species described herein, attaining a much larger size, having a much thinner, flatter test and petals that distally are open (Figure 7). It is a common element in Holocene deposits in the Swan Estuary (Yassini and Kendrick 1988) and occurs in the Herschel Limestone, a unit of the same age, on Rottnest Island.

While Pliocene sediments occur extensively subsurface in the Perth Basin (Kendrick *et al.* 1991) only rare, indeterminate fragments of *Peronella* are known, unlike coeval sediments in the Eucla Basin, where *P. ova* is common. The dominant clypeasteroid that occurs within the subsurface Pliocene Ascot Formation in the Perth Basin is *Ammotrophus*, a genus restricted to southwestern Australia today. This form, however, is not present in the Roe Calcarenite in the Eucla Basin.

ACKNOWLEDGEMENTS

I am grateful to George Kendrick for helpful discussions, mollusc identifications and assistance in the field, and to Sue Radford, Jamie, Katie and Tim McNamara for help with collecting specimens in the field. Thanks to Kris Brimmell for the photography, Danielle Hendricks for drafting and Steve Donovan and Burt Carter for helpful comments on the manuscript.

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Figure 7 *Peronella lesueuri* (Valenciennes, 1841) from the Middle Holocene Herschel Limestone, Lake Baghdad, Rottnest Island, Western Australia: A, B, WAM 77.516; x1.

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Aspects of female reproductive biology of two southwestern Australian *Temognatha* species (Coleoptera: Buprestidae)

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Abstract – Oviposition behaviour is described for the first time in a *Temognatha* species, *T. chalcodera* (Thomson, 1878). *Allocasuarina acutivalvis* (F. Muell.) L. Johnson subsp. *acutivalvis* (Casuarinaceae) is the first recorded larval hostplant for *T. chalcodera*. Pre-oviposition behaviour is described for the first time in *Temognatha bruckii* (Thomson, 1878) and *T. chalcodera*. In-situ photos of *T. chalcodera* oviposition and *T. bruckii* pre-oviposition behaviour are provided. The published literature on pre-oviposition behaviour in *Temognatha* is reviewed. The *Temognatha variabilis* species-group is defined and diagnosed. Possible reasons for evolution of the apomorphic oviposition/pre-oviposition behaviour in these species are discussed.

INTRODUCTION

Temognatha Solier, 1833 is a moderately large Australian stigmoderine genus of ca. 85 valid known taxa, the bionomics of which are poorly known. In this paper I present the first observations of *Temognatha* oviposition, in *T. chalcodera* (Thomson, 1878), and pre-oviposition behaviour in *T. chalcodera* and *T. bruckii* (Thomson, 1878). All observations are based on recent fieldwork I have undertaken at a single site 18 km east of Yellowdine, Western Australia (31°17'S, 119°50'E). At this site the *Temognatha chalcodera* and *T. bruckii* observations were made 25 m apart. During the course of observations, I was able to take a number of in-situ photos of *T. chalcodera* oviposition and *T. bruckii* pre-oviposition behaviour, and the most informative photo of each is provided. I also review the little that has been published on "pre-oviposition" behaviour in the genus.

Zoological specimen measurements linear, measured to nearest 0.05 mm using Zeiss stereomicroscope ocular micrometer (0–10 mm) or calipers (1–20 cm). Botanical specimen measurements linear, measured to nearest 0.05 mm using calipers or nearest 1 mm using tape measure. Buprestid morphology measurement definitions and their text abbreviations (capitalized in brackets) as follows: total length (TL) – from front of head (between antennae) to elytral apex; head width (HW) – to outer margins of eyes in frontal view; minimum interocular distance at vertex (MIDAV).

OBSERVATIONS

Temognatha (*Temognatha*) *bruckii* (Thomson, 1878)

Figure 1

Three female adults observed on 26 January 1990, at 1410–1515 hrs. All were "charcoal-scraping" 0.5–1.7 m above ground on two dead tree stumps (plant taxon unidentifiable) that were burnt on one side.

First female (TL: 29.2 mm) observed "charcoal-scraping", at 1410–1432 hrs. It was initially located by the sound of its scraping, audible for 1.5 m. This individual was 0.9 m above ground on south face of a 2 m high tree stump, and its body was positioned with longitudinal axis parallel to the ground. It had used its legs to raise the forepart of its venter off the stump surface, while simultaneously curving sternites 5, 6 and 7 ventrally so that the extruded ovipositor and sternite 7 apex made contact with the stump surface. It then walked transversely across the charcoal patch (burnt area), while in this raised posture, and scraped and picked up charcoal particles into its ovipositor by using the combined action of its ovipositor and sternite 7 apex. After completing one scrape, it faced the opposite direction (180° to the direction of the previous scrape) and repeated the process, thereafter constantly alternating the direction of scrapes. Each unidirectional scrape lasted 2–3 sec., with the ovipositor remaining in contact with the charcoal surface for 1–2 cm maximum width. This female



Figure 1 *Temognatha bruckii* female charcoal-scraping (showing combined action of ovipositor and sternite 7) at 1425hrs on fire-blackened tree stump, 18km east of Yellowdine, Western Australia. Photo: author.

continuously scraped charcoal on this stump until 1415 hrs, after which it flew to a second blackened stump (1.2 m high) 8 m south of the first. Adopting the same posture and methods it continued charcoal-scraping 0.5 m above ground for a further 15 min., on north side of second stump (Figure 1). It ceased scraping at 1432 hrs and took flight to north-west.

Two more females were observed, at 1443 hrs, flying in from south-east and landing on first stump used by previous female. One landed 0.9 m above ground, while the other landed 1.7 m above ground. Their choice to use the first scraping site of the previous female was obviously not based on making visual contact with already present individuals, since the first female had already left. They then simultaneously and continuously scraped charcoal into their ovipositors, from 1445–1515 hrs, mostly working parallel to the ground and using the same methods as the first individual. No further observations were made.

Temognatha (Temognatha) chalcodera
(Thomson, 1878)

Figure 2

Two female adults observed on 26 January 1990,

at 1525–1535 hrs. Each was ovipositing 6–7 cms above ground on living trunks of mature diminutive non-flowering *Allocasuarina acutivalvis* (F. Muell.) L. Johnson subsp. *acutivalvis* (Casuarinaceae).

First female observed, at 1525 hrs, to oviposit on trunk of an apparently healthy 1.6 m high *A. acutivalvis* plant. It laid a single subcircular egg (on south face of trunk) with maximum diameter of 4.0 mm, 6.7 cm above ground on outside of trunk surface (trunk diameter 1.8 cm at this level), and then immediately (almost simultaneously) completely coated the egg with cemented yellow sand, thereby roughly forming a hemisphere (maximum diameter 8.5 mm, maximum height 3.8 mm) glued to the trunk surface. The encased egg thus appeared as a small “cemented sand-dome” (composed of quartzitic sand grains with maximum size of 1.3 mm) attached to the bark. Oviposition lasted a total of 30 sec., whereupon this female walked down onto ground and was observed to scrape and pick up yellow sand into its extruded ovipositor using the combined action of its ovipositor and sternite 7 apex, as it slowly walked along. This female eventually disappeared into scrub.

Second female (TL: 35.8 mm) observed, at 1531



Figure 2. *Temognatha chalcodera* female ovipositing (showing sand being ejected onto egg) at 1532hrs on *Allocasuarina acutivalvis*, 18km east of Yellowdine, Western Australia. Photo: author.

hrs, flying and then landing on top of an apparently healthy 1.4 m high *A. acutivalvis* plant, 3 m south of first oviposition site. It then walked head-first to base of trunk at ground level, turned 180°, and returned up trunk for a short distance to begin ovipositing at 1532 hrs (Figure 2). It laid a single subcircular egg (on east face of trunk) with maximum diameter of 4.7 mm, 7 cm above ground on outside of trunk surface (trunk diameter 1.3 cm, at this level), and then immediately completely coated the egg with cemented yellow sand, thereby forming a roughly hemispherical cemented sand-dome (maximum diameter 7.7 mm, maximum height 3.7 mm) composed of quartzitic sand grains with a maximum size of 1.0 mm. Oviposition duration as in previous individual.

In both instances the appearance of the domes contrasted strongly with the coloration and texture of the stems to which they were attached.

A search of the surrounding area revealed numerous fresh domes, of similar size and appearance, attached to the surface of the lower branches and trunk bases of other living and apparently healthy *A. acutivalvis* plants (with and without seed cones), including mature individuals up to 3 m high. Some living plants had disintegrating domes scattered over their stems

and branches, but no emergence (exit) holes that could be attributed to adult beetles the size of *T. chalcodera*. There was no evidence that *T. chalcodera* oviposited on the few dead or dying *A. acutivalvis* plants in the area.

Sand was not present on the stem immediately under the centre (where the egg was/is located) of any old or fresh domes examined. However, a single 1.5–2 mm maximum diameter oval hole was present under the centre of some fresh domes, and was associated with a first instar buprestid larvae in one instance.

Occasional plants of *Allocasuarina corniculata* (F.Muell.) L.Johnson were also present at this site, but there was no evidence that *T. chalcodera* oviposited on this species. Interestingly, in this locality *A. acutivalvis* has smooth bark on its branches and trunk while *A. corniculata* has rough corrugated bark on same.

DISCUSSION

The presence of numerous fresh domes suggested *T. chalcodera* frequently oviposited at this locality during the 1989/1990 summer period. The occurrence of old and disintegrating domes on plants lacking adult emergence holes possibly

indicates failed larval development in previous years or prolonged development of larvae/pupae.

The presence of powdered or particulate material in the abdomen of female stigmoderine buprestids has been previously noted by three authors, although the purposes ascribed to this material and the hypotheses of its method of uptake and utilisation have differed.

Dodd (1913: 103–104; 1916: xxvi–xxvii) reported two or three little sacs containing fine sand “at the extreme tip of the abdomen” in dissected female *Temognatha regia* (Blackburn, 1892) (as *Stigmodera regia*) and observed females on the ground taking up sand into these sacs, although he was unable to determine the exact mechanism of sand uptake. As the females involved were old and contained few eggs, he suggested that the sand served as ballast to stabilize post-oviposition flight in females, in windy conditions.

Macqueen (1948: 1–2; 1964: 17) similarly reported powdered charcoal in the abdomen of *Temognatha fortnumi* (Hope, 1843) (as *Stigmodera* (*Thermognatha*) *fortnumi*), and observed females scraping their abdomens against charred timber, apparently taking in charcoal. These observations were made in “similar circumstances” to his earlier observations of presumed oviposition in the same species. In these earlier instances, females were observed probing among charred ironbark (*Eucalyptus* spp.) sapwood with their abdominal tips, although oviposition was not specifically observed. Macqueen (1948: 2) suggested that the eggs were coated with charcoal, in some manner, prior to oviposition.

Gardner (1990: 296) reported a posteriorly opening sac lying dorsal to the vagina and interposed between the dorsal valve and style-bearing valve of the stigmoderine ovipositor. She named this sac the “particle sac”, as it was often packed with charcoal, sand, or fragments of plants (Gardner, 1990:313). Gardner (1990: 313) further suggested that the short ovipositor of the Stigmoderini (with its heavily sclerotised spatulate setae) was an adaptation for excavating an oviposition depression in soil or host plants, that the particle sac filled with particles during the creation of this excavation, and that the eggs *may* be subsequently coated by material expelled from the sac. Gardner (1990: 296, 298–300) also reported the presence of a multilobed female accessory gland (in the median ventral surface of the vagina) in the genera *Temognatha*, *Calodema* and *Metaxymorpha* (one species-group). She suggested (1990:299) controlled release of the gland’s contents because of the presence of striated muscle penetrating between its lobes. Gardner (1990:319) also suggested as uses for the glandular secretion (at least partly composed of mucopolysaccharides) “an eggshell which hardens on contact with air to

protect against water loss or attack by bacteria or fungi; a toxin to discourage predators; an adhesive to make the eggs sticky so that they acquire a protective covering of particles or to cement the eggs to a substrate or to each other; a trophic substance; or a tropho-stimulant to encourage newly emerged larvae to eat their eggshells”.

The observations reported in this paper partially elucidate the function/use of the contents of the particle sac and female accessory gland in some stigmoderine buprestids.

The observations on charcoal-scraping by *Temognatha bruckii* extend those made for *T. fortnumi* by Macqueen and confirm that charcoal is taken up by the combined action of sternite 7 and ovipositor. Dodd and Macqueen had previously only established that material was taken in via the abdominal apex, although Macqueen (1948: 2; 1964: 17) had suggested that charcoal was powdered by the ventral plates of the abdomen and gathered by “short bristly hairs” around the anal opening.

The observations on *T. chalcodera* confirm the suggestions of both Macqueen and Gardner that the material in the particle sac may be used to cover the egg (*contra* Dodd), but differ in several features from their suggested mechanisms. Firstly, at least in *T. chalcodera*, the egg is covered by a protective dome of sand immediately after/during oviposition, not coated with it prior to being laid (Macqueen’s hypothesis). Secondly, in this species the material in the particle sac is clearly not collected by the female from the oviposition site, but is collected elsewhere prior to oviposition, and then transported in the particle sac to the oviposition site where it is ejected over the surface of the egg as part of the oviposition sequence. Thirdly, the eggs of *T. chalcodera* are laid on the surface of the stem/trunk, not in an excavation (either in the ground or host plant) as suggested by Gardner. While direct observations on oviposition in the charcoal-scraping species are lacking, the similarities in uptake of particles suggest a similar use for the material to that seen in *T. chalcodera*. In light of these observations, it seems likely that the spatulate setae on the style-bearing valve of the ovipositor of the Stigmoderini are involved in particle collection rather than any excavation for egg deposition (*contra* Gardner, 1990: 313). It also seems likely that the primary function of the accessory gland secretion is to “glue” the egg to the surface of the intended hostplant and to then cement particles ejected from the particle sac onto the remaining exposed surface of the egg. The accessory gland secretion may secondarily augment the role of the sand/charcoal coating on the eggs and perform some of the other functions suggested by Gardner.

The four species for which observations of oviposition and presumed pre-oviposition

behaviour are available are, co-incidentally, closely allied and members of the *Temognatha* (*Temognatha*) *variabilis* species-group, as defined herein. This species-group contains the following species: *T. variabilis* (Donovan, 1805) (type species of *Temognatha*), *T. fortunei* (Hope, 1843), *T. mitchellii* (Hope, 1846), *T. bruckii* (Thomson, 1878), *T. chalcodera* (Thomson, 1878), *T. regia* (Blackburn, 1892). The *T. variabilis* species-group is diagnosed by the following character combination: size moderately small to large (TL 19–46 mm); eyes strongly converging dorsally (MIDAV 10–33% of HW, sexually non-dimorphic intraspecifically); pronotum with explanate lateral margins; pronotal base same width as (not wider than) elytral base; scutellum shape scutiform (subpentagonal) to subcircular; elytra punctate-striate; epipleuron entire (non-serrate), without caudally directed ventral spur at level of hind-coxae, and only weakly expanded anterior to this level; elytron apex bispinose with narrow arcuate or broad truncate excision between spines (spine length reduced in some taxa); sternite 7 sexually dimorphic: females convexly rounded/more elongate, males concavely/arcuately excised (notched); presence on female sternite 7 of an arcuate subapical carina (parallel to and near apical margin) with dense subapical setae; female proctiger comprised of completely fused epiproct and paraprocts, without discernible suture between both; male proctiger comprised of incompletely fused epiproct and paraprocts, with visible suture between both; basal hind-tarsomere length 1–1.5x that of following hind-tarsomere; tarsal claws moderately to strongly curved and with weak to strong basal lobes (intraspecifically constant); 19–56 tubules per testis (*bruckii* and *fortunei* not examined for this character); “shape” of male genitalia; ovipositor broad (wider than long), dorsal valve longitudinally striate dorsally, ventral valve not strongly sclerotized ventrally.

On the limited data known (this paper; pers. obs.; $n = 3$ species), members of the *T. variabilis* species-group breed in *Allocasuarina* spp. (*contra* Macqueen: 1948; 1964). In the discussion following Macqueen's (1948) observations there is mention (p.3), probably attributable to A.P. Dodd, that *T. regia* “breeds near the base of Casuarinas”. In the absence of observations of reproduction in other members of this species-group and other *Temognatha* taxa, the phylogenetic generality of the behavioural characteristics discussed herein is indeterminate. Variation in *Temognatha* ovipositor form/structure (see Peterson, 1991: 121,123, figs 2–4) may be indicative of alternative mechanisms of particle collection/oviposition in other *Temognatha* species. However, the slight structural modifications of female sternite 7 within the *T. variabilis* species-group are likely to relate to sand/

charcoal-scraping, and thus this latter habit (in conjunction with the unusual egg-laying behaviour) may be characteristic of this species-group. Additional observations are required to determine the extent and constancy of species-level differences in the type of particles collected.

The functional significance of covering the egg with sand (aside from the confirmed function of aiding glueing of egg to trunks of plants), and possibly charcoal, is unknown. In the interests of stimulating further research, I propose three potential functions for the sand-covering, acting singly or in combination: protection against parasitism/predation of egg; protection against desiccation of egg; thermoregulation to maximise rate of development of egg to first instar larva.

Additionally, the nature/duration of this type of oviposition behaviour is likely to place adult females at less risk from predation, which would be increased if they had to spend extra time to penetrate the tough non-fissured living bark to lay eggs. This type of oviposition also puts the onus on the larvae to penetrate into the hostplant and thus suggests it is likely to be more energy efficient because of the following factors: larval mandibles are presumably better designed to penetrate living unfissured bark/timber than the “reduced” stigmoderine ovipositor; the hole created by first instar larva is smaller (only required to be width of larval pronotum, the widest part of larval body) than that required to oviposit an egg into.

Three major types of oviposition behaviour have been previously described in the family Buprestidae: exophytic (egg laid directly into soil so larva, upon hatching, can feed externally on roots while initially protected by soil: Julodini (Holm, 1979: 98; Holm and Gussmann, 1992: 3), *Julodimorpha bakewelli* (White) (Hawkeswood and Peterson, 1982: 242)); simple endophytic (egg laid directly into crevices/fire-scars in timber/bark, or into leaf/stem tissue so larva, upon hatching, can feed internally on cambium, bark or leaves/stems while initially protected by timber/leaf/stem surface: majority of buprestid genera (e.g. Hadlington and Gardner, 1959: 325, 326)); complex endophytic (egg laid on surface of leaf/stem or timber/bark and covered by a presumably protective coating of material until larva hatches and bores into hostplant: *Agrilus obtusus* Horn (Manley, 1977: 80, fig.2.)).

The behaviour described in this paper generally conforms to the latter oviposition method, which I consider ecologically intermediate between the two former oviposition types. However, Manley's observations differ from mine in being apparently based on captive beetles, and *A. obtusus* adults utilize their own faeces to provide a mat to lay the egg on, and to then cover and presumably camouflage exposed parts of the egg. This suggests

that *Temognatha chalcodera* oviposition behaviour is even more derived than that previously described, since this taxon utilizes non-hostplant material to coat the egg, and the ovipositor has special receptacles to store this material. There are two independent aspects of *T. variabilis* species-group larval/oviposition behaviour which may have resulted in the evolution of their apomorphic oviposition type: the larval requirement to utilize living unfissured timber/bark; the lack of suitably sized crevices/fire scars in the larval host plants to accommodate the large eggs. The available data suggest that this novel oviposition behaviour has primarily evolved to allow *T. chalcodera*, and possibly other *T. variabilis* species-group taxa, to internally access (in an energy-efficient manner) living hostplants independent of heat/fire-created access routes, though structural/physiological and ecological studies of their larvae are required to confirm this. Finally, the precise mechanisms of site selection (presumably based on visual or olfactory cues, or both) are unknown for ovipositing *T. chalcodera* and charcoal-scraping *T. bruckii* females.

ACKNOWLEDGEMENTS

I thank Dr G.M. Shea (Sydney) for assistance with some aspects of manuscript preparation.

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Manuscript received 24 July 1994; accepted 13 November 1996.

Early Cambrian stenothecoid molluscs from China

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Abstract – A new species of *Stenothecoides*, *S. yochelsoni* sp. nov., is described from the Early Cambrian Huangshandong Member of the Tongying Formation in Eastern Yangtze Gorge, western Hubei, China. This species is one of the new members of the Yangtze micromolluscan fauna. The occurrence indicates that the first appearance of *Stenothecoides* can be dated to the earliest Cambrian, and it is probably the earliest record of the genus. Two other Early Cambrian species, *Bagenovia* cf. *sajanica* Horny and *Stenothecoides* sp., are described from the Xidashan Formation of Kuruktag, Xinjiang, China.

INTRODUCTION

In 1979, the writer while making a study of the earliest Cambrian molluscs from the Eastern Yangtze Gorge of western Hubei, China, recovered from acid-residues from the Huangshandong Member of the Tongying Formation of the Tianzhushan Section, an undescribed species of *Stenothecoides*. The Tianzhushan Section is located at the west side of the Dianziliang Primary School at Tianzhushan, Liantuo, about 25 km northwest of the city of Yichang. The Huangshandong Member, a richly fossiliferous unit, is composed mainly of purplish brown arenaceous-rudaceous dolomites, intercalated with striped siliceous phosphorites, about 1.88 m in thickness. It conformably overlies the Precambrian Baimatuo Member of the Tongying Formation and is overlain disconformably by the Early Cambrian Shuijingtuo Formation (Zhao *et al.* 1980).

The material in the arenaceous-rudaceous dolomites was preserved in association with other elements of the Yangtze micromolluscan fauna, such as *Tchangsieichiton notabilis* Yu, *Sinoconus clypeus* Yu, *Yangtzeconus priscus* Yu, *Obtusoconus rostriptutea* (Qian), *Purella tianzhushanensis* Yu, *Igorella hamata* Yu, *Archaeospira ornata* Yu, *Maclurites hubeiensis* Yu and *Heraultipegma yunnanense* He and Yang (Yu 1979, 1984a, b, 1985, 1987, 1990; Qian, Chen and Chen 1979; He and Yang 1982). Of all the micromolluscs, the most interesting and characteristic forms are *Y. priscus*, *A. ornata*, *O. rostriptutea*, *I. hamata* and *H. yunnanense*. These fossils are widely distributed in the Meishucunian Stage in eastern Yunnan, western Sichuan and in corresponding beds in many parts of the Yangtze Platform.

Bagenovia cf. *sajanica* Horny and *Stenothecoides* sp. were collected in 1978 by Zhang Sengui, Nanjing

Institute of Geology and Palaeontology, Academia Sinica, from the base of the Early Cambrian Xidashan Formation on the northern slope of Mohurshan of the Kuruktag Mountains, Xinjiang, China. On the basis of palaeontological and lithological characteristics, the Early Cambrian of this area has been divided into two formations: in ascending order, the Xishanbuluk Formation and the Xidashan Formation (Zhang 1983).

The Xidashan Formation is about 88 m in thickness (Zhang 1983). It is composed chiefly of blackish-grey, arenaceous limestones and argillaceous limestones with a basal bed of purplish-grey, arenaceous, lenticular limestone. The basal bed yields a rich fauna of trilobites and archaeocyathids and some monoplacophorans, gastropods, brachiopods and hyolithids. Stenothecoids are rare within the fauna of the Xidashan Formation, only three specimens being obtained; however these include two species placed in two genera, namely: *Bagenovia* cf. *sajanica* Horny and *Stenothecoides* sp. In association with them are the trilobites *Metaredlichioidea rectangularis* Zhu and Lin, *Chengkouia xinjiangensis* Zhu and Lin (Zhu and Lin 1983); the archaeocyathids *Aldanocyathus* cf. *belvederi* (Rozanov), *Coscinocyathus xinjiangensis* Zhang (Zhang 1983) and the molluscs *Eocyrtolites radiatus* Yu and *Cyrtodiscus? kuruktagensis* Yu (Yu, 1986). Among the associated fossils, the genera *Metaredlichioidea* and *Chengkouia* are zonal fossils of the *Metaredlichioidea*–*Chengkouia* zone. This zone is widely distributed in the Middle Tsanglangpu Stage of southeastern Shaanxi, northwestern Sichuan and eastern Guizhou (Zhou and Yuan, 1980). Therefore, the basal part of the Xidashan Formation is considered to be middle Early Cambrian, equivalent to the Middle Tsanglangpu Stage in eastern Southwest–Central

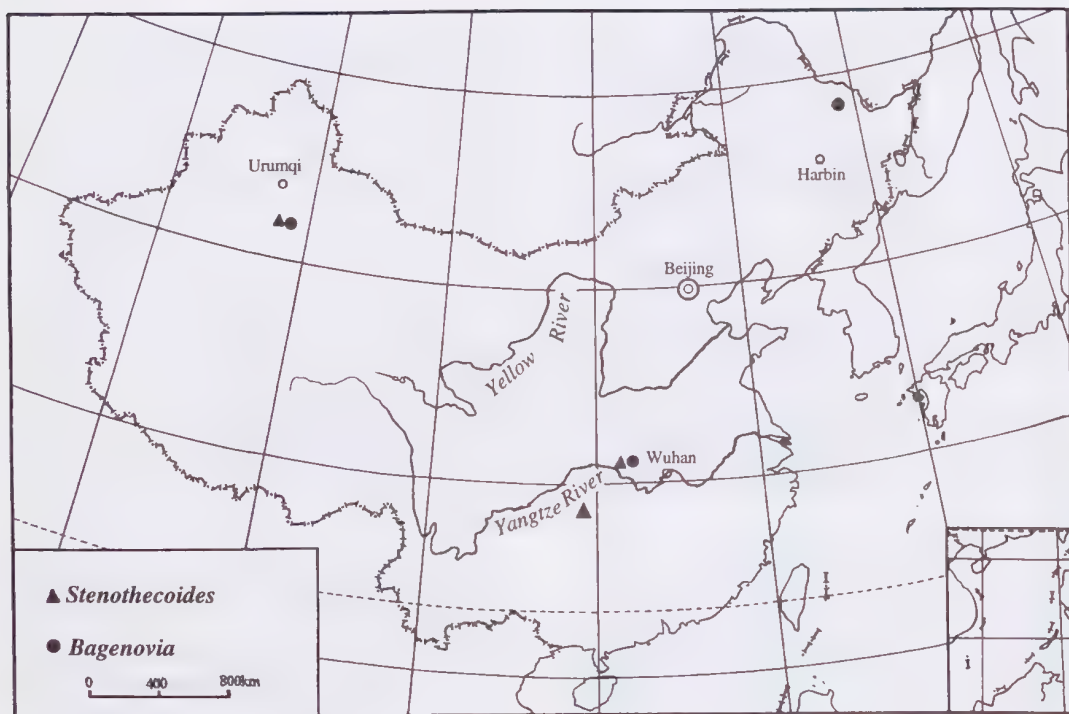


Figure 1 Sketch map showing the fossil localities.

China (Zhang 1983; Zhu and Lin 1983; Yu 1986).

Specimens described in this paper are all deposited at the Nanjing Institute of Geology and Palaeontology, Academia Sinica.

STENOTHECOIDES AND BAGENOVIA

Stenothecoides has mainly been reported from the Early Cambrian of east Greenland (Poulsen 1932), Laborador and Yukon Region of Canada (Resser 1938, Yochelson 1968, 1969), Siberia (Horný 1957; Missarzhevsky in Rozanov and Missarzhevsky 1966; Aksarina 1968, Aksarina and Pelman 1978), central Kazakhstan (Koneva 1979) and western Mongolia (Zhegallo 1982), and the Middle Cambrian of United States (Walcott 1884, 1886; Robison 1964), British Columbia of Canada (Rasetti 1954), central Kazakhstan (Koneva 1979) and central North Greenland (Peel 1988). During the last two decades, this genus has been extensively found in China. It has been collected from the Huangshandong Member of the Early Cambrian Tongying Formation of Eastern Yangtze Gorge, western Hubei, the Early Cambrian Xidashan Formation of Kuruktag, Xinjiang and the Early Cambrian Tianheban Formation of Xianfeng of Hubei and other places (Figure 1). Of the material from these formations, that from the Eastern Yangtze Gorge is a bivalved, asymmetrically

inequivalve form. According to previous records, most species of the genus *Stenothecoides* occur only as a single non-articulated valve. Only a few species were preserved in a bivalve condition, e.g., *Stenothecoides knighti* Yochelson (1969: 59–60, fig. 2) from the Early Cambrian of Yukon, Canada, *S. siberica* (Aksarina) (Aksarina and Pelmen 1978: 115, pl. XVII, figs. 4–6) from the Early Cambrian Lenian Stage of Siberia, *S. bellus* Koneva (1979: 26, pl. V, fig. 1) from the Early Cambrian Lenian Stage of central Kazakhstan and *Stenothecoides* sp. (Yochelson 1969: 51, fig. 1) from the upper Early Cambrian of Siberia.

So far as I am aware, most of the Early Cambrian species of *Stenothecoides* are associated with trilobites or archaeocyathids. However, the new species of *Stenothecoides* described herein is found with a micromolluscan fauna that predates the trilobites. It therefore possibly represents the earliest record of *Stenothecoides*. Therefore, the first appearance of *Stenothecoides* can be traced back to the very earliest Cambrian. Furthermore, it is a new member of the Yangtze micromolluscan fauna, which occurs in the earliest Cambrian Meishucunian Stage of the Yangtze Platform in China. As such it is the first biomineralisation event in the evolutionary history of invertebrates in the Phanerozoic. It also represents the first stage of the diversification in the history of Phylum

Mollusca. The fauna consists of the genera *Yangtzechiton* and *Luyanhaochiton* (Polyplacophora); *Yangtzeimerisma* and *Merismoconcha* (Merismoconchia); *Eosoconus* and *Archaeotremaria* (Monoplacophora); *Yangtzespira* and *Archaeospira* (Gastropoda); *Yangtzedonta* (Bivalvia) and *Heraultipegma* (Rostroconchia) (Yu 1979, 1984 a, b, 1985, 1987, 1990; Jiang in Luo *et al.*, 1982; He and Yang 1982). The new species of *Stenothecoides* described herein, like other Meishucunian micromolluscs, is characterized by its tiny shell. In general, the usual size of *Stenothecoides* is 4–10 mm in length, though specimens can reach a length of 14 mm or so. However, the Meishucunian species is 1.1 mm long.

The discovery of *Stenothecoides* from the Meishucunian Stage provides important material evidence for study of the origin of Stenothecoida and the evolutionary relationship with other molluscs. Of special interest is that most Early Cambrian species of *Stenothecoides* possessed a distinct ridge or fold on the dorsal valve or right valve of variable expression (Rasetti 1954; Yochelson 1969; Koneva 1979; Peel 1988), while in the Middle Cambrian, only a few species have a ridge on the valve. The new species of *Stenothecoides* has a thick ridge on the dorsal valve, occupying more than one-third the width of the valve. These characteristics indicate that this species is a primitive species of the genus *Stenothecoides*.

It is worth noting that the upper part of the Huangshandong Member bears a rich micromolluscan fauna. The polyplacophorans, monoplacophorans, gastropods and rostroconchs either lived a benthonic, creeping life within the subtidal and intertidal zone or were infaunal deposit feeders. Most shells are preserved incompletely, some overlap with each other, while some are fragmentary. These characters show that they were deposited in the turbulent flow of a shallow sea or even in the littoral zone.

One of the forms of stenothecoids in the Xidashan Formation at Kuruktag, Xinjiang is *Bagenovia* cf. *sajanica*. Horný in 1957 named the genus taking *Bagenovia sajanica* Horný as the type species. *Bagenovia sajanica* was first reported from the Early Cambrian of west Sayan, Siberia. This genus has been found in the Early Cambrian of Siberia (Radugin 1937; Horný 1957; Sytchev 1960; Aksarina and Pelmen 1978) and the Early Cambrian Lenian Stage of central Kazakhstan (Koneva 1976, 1979). In China, it has been found in the Early Cambrian Xidashan Formation of Kuruktag, Xinjiang, the Early Cambrian Wuxinzhen Formation of Yichun, Heilongjiang and the Early Cambrian Shipai Formation of Suizhou, Hubei. Two specimens were procured from the Xidashan Formation, including one covered with

radiating costae and one well-preserved internal mould with internal structures.

The internal structures of the valve consists of four pairs of asymmetrically arranged ridge-like impressions and three concentric impressions visible on the dorsal valve of the internal mould (Figure 3). The structure may correspond to anatomical features, but the soft tissues of stenothecoids are quite unknown. Since they have no expression of the outer surface and the direction of the ridge-like impressions are the reverse of the radiating costae, it seems likely that they reflect the impressions of some organs of the animal. The function of the internal structures is, however, difficult to interpret. It might be assumed that they either had a direct effect on their free movement or, alternatively, relate to the control of the opening and closing of the valves or some other physiological action, perhaps representing muscle attachments (Yochelson 1969).

The taxa *Bagenovia* cf. *sajanica* and *Stenothecoides* sp. co-occur with shallow and warm water fossils, such as archaeocyathids and the trilobite *Metaredlichnoides* and *Chengkouia*. Most specimens of archaeocyathids, trilobites, brachiopods and molluscs are preserved incompletely, some of them disorderly preserved in the limestone, others as fragments (Zhang 1983). These characteristics indicate that the fauna reflects a shallow water carbonate facies, perhaps deposited in a epicontinental sea. Their associated sediments, arenaceous limestone, are characteristic of shallow water deposition.

SYSTEMATIC PALAEONTOLOGY

Class Stenothecoida Yochelson, 1968

Superfamily Cambridiacea Horný, 1957

Family Cambridiidae Horný, 1957

Genus *Stenothecoides* Resser, 1938

Stenothecoides yochelsoni sp. nov.

(Figure 2 A–F)

Holotype

NIGP 116387, in the collections of the Nanjing Institute of Geology and Palaeontology, Academia Sinica, collected by the writer in 1978 from Huangshandong Member of the Early Cambrian Tongying Formation at Tianzhushan of Yichang, Hubei, China.

Diagnosis

Tiny, bivalved, asymmetrically inequivalved, narrowly elongated, about one-third as wide as long. Two valves closed very tight, commissural line curving slightly downward. Conjoined line not known in detail. Apical area high, curves

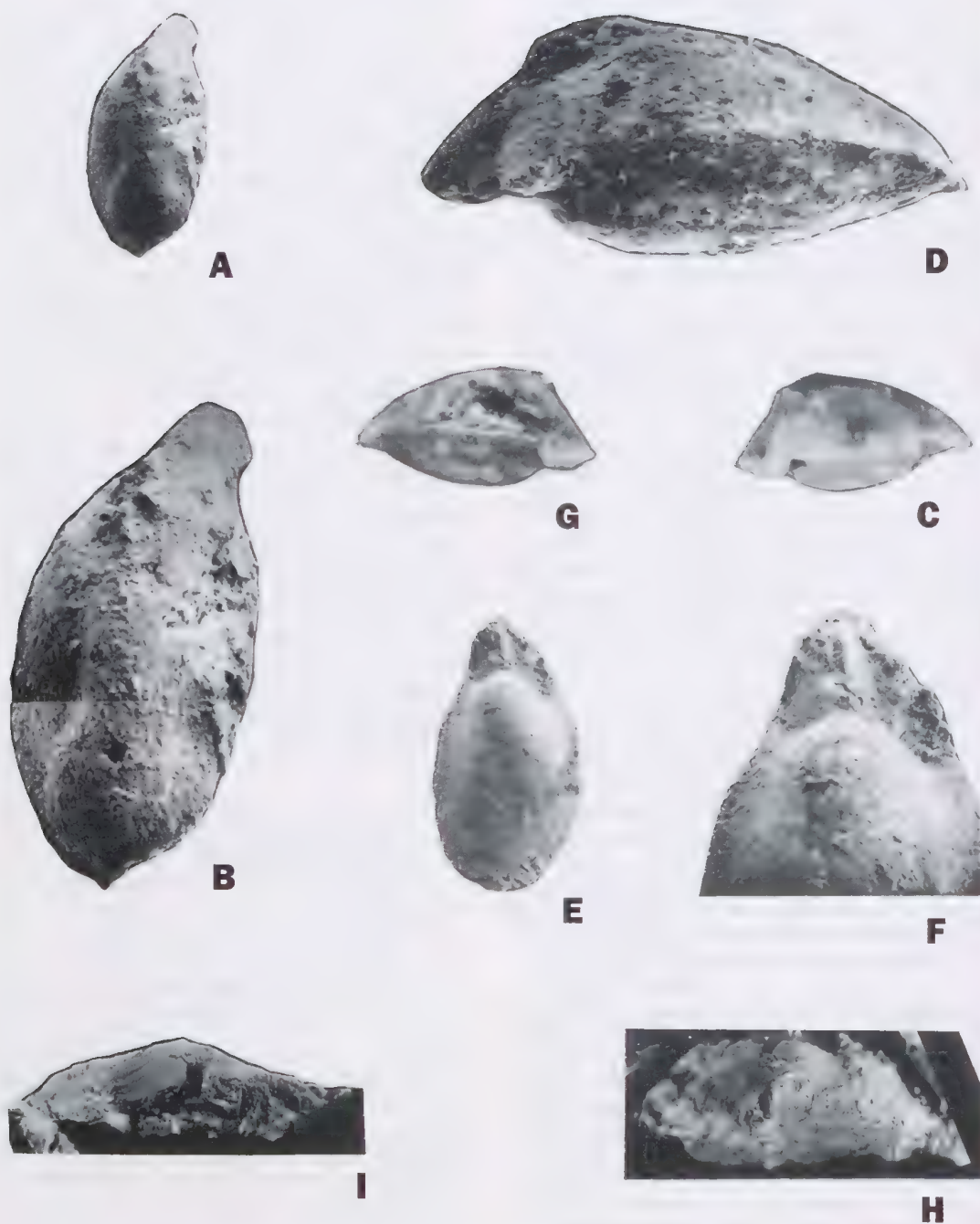


Figure 2 A–F. *Stenothecoides yochelsoni* sp. nov. NIGP 116387, Huangshandong Member of Early Cambrian Tongying Formation, Tianzhushan of Yichang, Hubei, A. plan view, x 40. B. enlargement of dorsal valve, showing thick ridge and other internal structures, x 80. C. left side view, x 40. D. enlargement of left side, showing the commissural line, x 90. E. plan view, x 40. F. enlargement of ventral plan view, x 80. G. right side view, x 40. H–I. *Stenothecoides* sp. NIGP 116391, Xidashan Formation, Kuruktag Mountains, Xinjiang, plan and lateral views, x 4.

anticlockwise during growth, strongly protruding and overhanging adapical margin. A prominently thick ridge starting from apical area, extending and widening to the abapical margin. Ventral valve smaller and lower than the dorsal one. Apex large, strongly rounded.

Description

Shell very tiny, 1.1 mm long, 0.45 mm high and 0.5 mm wide; bivalved, asymmetrically inequivalved and narrowly elongated, about one-third as wide as long. Two valves closed very tight, commissure of valves simple, commissural line curving slightly downward, in particular anteriorly and posteriorly. Conjoined line not known in detail. Apical area strongly arched. Dorsal valve high, strongly arched, the apex being at about one-third of the length. Apical area high, strongly protruding and overhanging the adapical margin and curving anticlockwise during growth. A prominently thick ridge starting from the apical area, extending backward for about two-thirds the total length and then abruptly expanding and widening to the abapical margin. The ridge is bordered by two narrow furrows, occupying about one-third the width at the middle part of the dorsal valve and then almost the whole part at the end. The lateral slopes slightly depressed and then oblique to the lateral margins.

Ventral valve smaller and lower than the dorsal valve. Apex large, strongly rounded and convex, gradually sloping toward the abapical margin. The lateral slopes of the apex abruptly convex and then flatten to the margin.

The surface character is unknown, except for some granules in the dorsal valve.

Remarks

Judging from the general morphological characters of the shell, *Stenothecoides yochelsoni* sp. nov. is similar to *S. knighti* Yochelson (1969: 59–60, figure 2) from the Early Cambrian of Yukon, Canada. They share such common features as: the asymmetrically bivalve shell, the possession of a prominent ridge on the dorsal valve; and simple commissure of the valves. However, there are still great differences between *S. yochelsoni* and *S. knighti*, essentially in the shell being narrowly elongated in dorsal valve view in the former, but subelliptical in dorsal valve view in the latter; in *S. yochelsoni* the commissural line is curving slightly downward, whereas in *S. knighti* the commissural line is curving slightly upward; in the dorsal valve of *S. yochelsoni* the apical area is strongly protruding and overhanging the adapical margin, but in *S. knighti*, the apical area is low, slightly overhanging the ventral valve; in the former, the dorsal valve is strongly arched and has a prominently thick ridge beginning from the apical

area, extending backward for about two-thirds the total length and then abruptly expanding and widening to the abapical margin, while in the latter, the dorsal valve is low and has a narrow ridge; in *S. yochelsoni* the ventral valve is small and low, with a large and rounded apical area, but in *S. knighti*, the ventral valve is relatively convex and with a curved ridge.

In possessing a narrowly elongate valve, *S. yochelsoni* is closely related to *Stenothecoides* sp. (Yochelson 1969: 51, figure 1) from the upper Lower Cambrian of Siberia, but it is strongly distinguished from Siberian species in the more convex dorsal valve, the less convex ventral valve, in the presence of a distinctly thick ridge on the dorsal valve and the more protruded apical area.

In some respects this species resembles *Stenothecoides bellus* Koneva (1979: 26, pl. V, fig. 1) from the Early Cambrian Lenian Stage of central Kazakhstan. It differs from the latter in the more narrowly elongated shell; the thicker ridge, the more protruded apical area and in the smaller ventral valve.

Etymology

The specific name is in honour of Dr Ellis L. Yochelson of the Department of Paleobiology, National Museum of Natural History, Washington D.C., U.S.A.

Occurrence

Upper part of the Huangshandong Member of the Early Cambrian Tongying Formation at Tianzhushan of Liantuo, Yichang, Western Hubei.

Stenothecoides sp.
(Figure 2 H–I)

Material

A single specimen, NIGP 116391, in the collections of the Nanjing Institute of Geology and Palaeontology, Academia Sinica. Collected by Zhang Sen-gui in 1978 from the base of the Early Cambrian Xidashan Formation on the northern slope of the Mohurshan of the Kuruktag Mountains, Xinjiang, China.

Description

Shell of large size, 13 mm long and 6 mm wide; asymmetric, fairly elongately ovate in plan view. Apex sharply pointed, distinctly protruding and overhanging the adapical margin and curving anticlockwise during growth. In plan view the valve is convex and tends to be most pointed at the adapical margin; narrowly rounded abapical margin and somewhat bent to right. Sides unequally convex, with the greatest width of the valve at about one-third of the length.

Surface of the shell ornamented by prominent, irregularly spaced coarser or finer growth lines.

Remarks

Although *Stenothecoides* sp. from the Early Cambrian Xidashan Formation in Kuruktag is an incomplete specimen, it represents a bivalved stenothecoid with distinct characteristics: the narrowly elongated and asymmetrical dorsal valve; the apex curves anticlockwise during growth and with irregularly spaced growth lines. This species should be unquestionably assigned to the genus *Stenothecoides*.

This form is very similar to *Stenothecoides* sp. from the upper Lower Cambrian of Siberia (Yochelson 1969: 51, figure 1) in such characters as the narrowly elongated dorsal valve, the pointed apex and the convex dorsal valve, but differs from the latter in the proportion between the length and width of the valve, in the more rounded posterior and in the coarser growth lines. In plan view, this species somewhat resembles *Stenothecoides carinatus* Koneva (1979: 27–28, pl. VI, figs. 5, 6) from the Early Cambrian Lenian Stage of central Kazakhstan, differing in the slender and more curved valve, in the narrower abapical margin and in the irregularly spaced growth lines. It is also allied to *Stenothecoides elongata* (Walcott) (1886: 129, pl. 12, figs. 4 a–b (not figure 4); Resser 1938: 24; Rasetti 1954: 63, pl. 11, figs. 3, 4), but differs from the latter in the more bent dorsal valve, in the wider abapical margin and in the irregularly spaced growth lines.

Occurrence

Basal part of the Early Cambrian Xidashan Formation of Mohurshan, Kuruktag Mountains, Xinjiang, China.

Genus *Bagenovia* Horný, 1957

Bagenovia cf. *sajanica* Horný, 1957 (Figures 3, 4 A–I)

Bagenovia sajanica Radugin, 1937: 301, fig. 5, (nomen nudum).

Bagenovia sajanica var. *raricostata* Radugin, 1937: 301, fig. 5a (nomen nudum).

Bagenovia sajanica Horný, 1957: 428, pl. III, figs. 1–6; Knight and Yochelson, 1960: 183, fig. 50, 8.

Bagenovia multicostata Yu, in Zhang, 1983: 10 (nomen nudum); Gao *et al.*, 1984: pl. IX, figs. 6, 9 (nomen nudum); Yu, 1986: 10 (nomen nudum).

Material

Three specimens, NIGP 116388–116390 in the

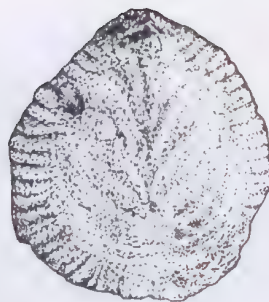


Figure 3 *Bagenovia* cf. *sajanica* Horný, showing the internal structures, X 8.

collections of the Nanjing Institute of Geology and Palaeontology, Academia Sinica. NIGP 116388 and 116389 were collected in 1978 by Zhang Sengui from the base of the Early Cambrian Xidashan Formation on the northern slope of the Mohurshan of the Kuruktag Mountains, Xinjiang, China. NIGP 116390 in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, was collected by a geological party from the Geological Bureau of Hubei from the Early Cambrian Shipai Formation of Suizhou, Hubei, China.

Diagnosis

Subcircular, slightly asymmetrical, apex pointed, slightly curved anticlockwise during growth, with twenty-two pairs of radiating costae from the flat keel. There are four pairs of asymmetrically arranged ridge-like impressions and three concentric impressions visible on the dorsal valve of the internal mould.

Description

Valve of medium size, slightly asymmetrical. Moderately convex, subcircular in plan view. Apex small, pointed, distinctly protruding and overhanging the adapical margin; slightly curved anticlockwise during growth. In plan view, the individual valve tends to be narrowly rounded adapically, broad rounded abapical margin, with the greatest width of the valve at about one half of the length. A distinctly flat keel situated near the median part of the dorsal valve, which gradually flattens and widens to the abapical margin. From the flat keel about twenty-two pairs of costae radiate. They are small and short in the adapical part, with sharp crests, separated by wider depressions and curved forward, gradually becoming larger and longer in the middle part and gradually crowded, indistinct abapically, with obtusely rounded crests and separated by the narrower depressions. Radiating threads which can be observed in the flat keel very fine and dense (Fig. 4B). Growth lines very fine and undulating;

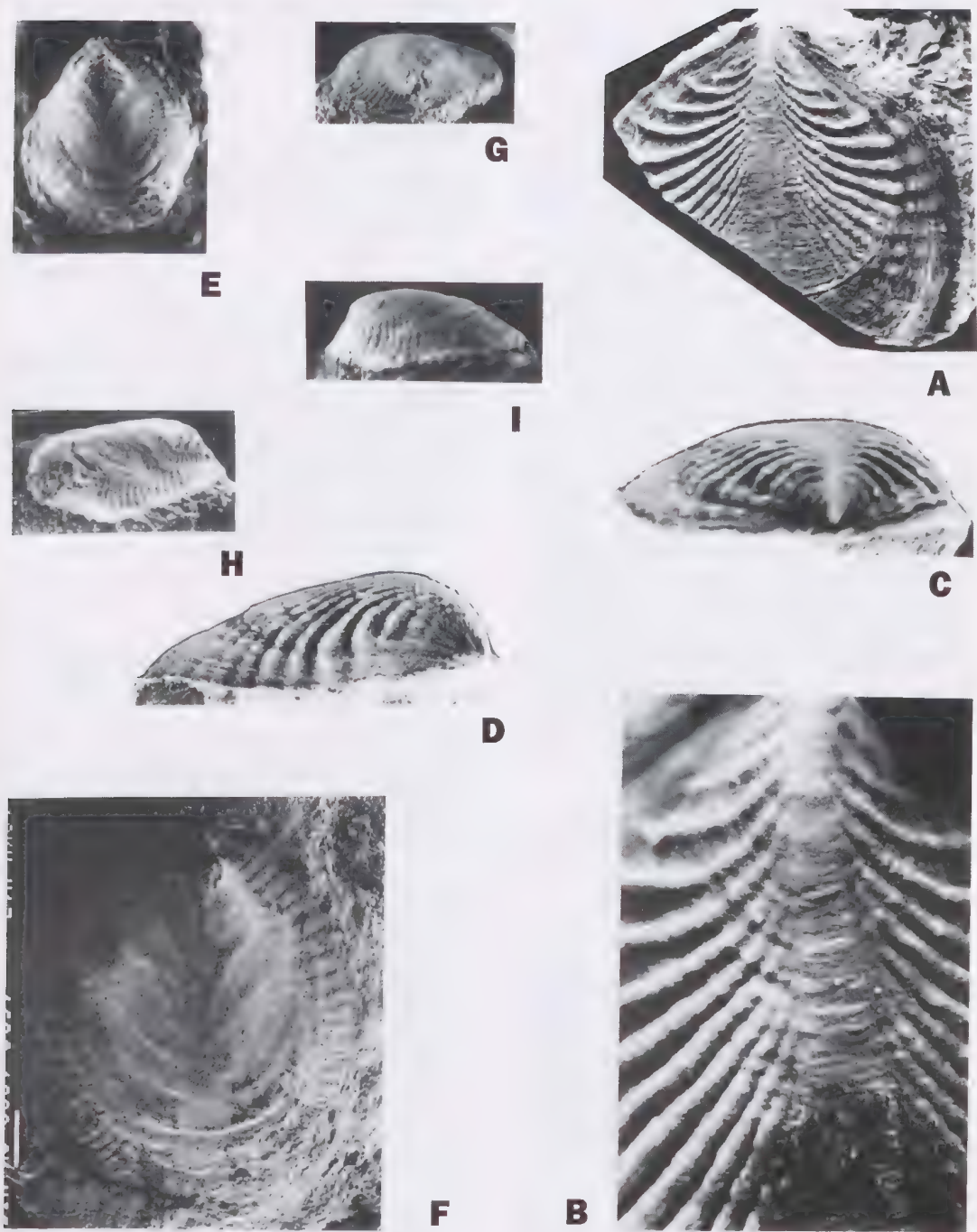


Figure 4 A-I, *Bagenovia* cf. *sajanica* Horný. A-D, NIGP 116388, Xidashan Formation, Kuruktag, Xinjiang. A. plan view, $\times 5$. B. enlargement of dorsal keel, showing the cancellated sculpture, $\times 15$. C-D. adapical and lateral views, $\times 5$. E-I, NIGP 116389, E, plan view, $\times 6$. F. enlargement of valve, to emphasize the internal structures, $\times 12$. G-I. adapical, right and left side views, $\times 5$.

crossed by the radiating threads to form a cancellated sculpture. With the increase in shell size, the growth lines become progressively thicker, and the radiating threads more and more obscure on the margin of the valve.

Shown in Figure 4 E-I is a nearly completely preserved internal mould. In plan view the valve appears subcircular and the apex is slightly broken. The traces of radiating costae can be seen on the margin of the valve. In the centre of the valve there is a longitudinal shallow depression, starting from the apex and gradually disappearing to the posterior. On the sides of the longitudinal shallow depression there are about four pairs of asymmetrically arranged ridge-like impressions and three concentric impressions (Figure 3). The direction of the ridge-like impressions is the reverse of the surface radiating costae. The first pair of ridge-like impressions are short and very obscure, situated near the apex. The second pair are situated at about two-fifths of the valve length from the adapical margin and gradually extended forward and inclined to the adapical margin; the left ridge-like impression is longer, and narrower than the right one. The third pair are similar morphologically to the second pairs, situated at the mid-length of the valve but longer and larger. The fourth pair is fainter and more obscure than the others, which is situated at about two-thirds of the valve from the adapical margin. The outer concentric impression is thin, forming a ring on the periphery. The middle one is stronger and shorter than the others; while the inner one is faint, gradually extending to the adapical side.

Dimensions (in mm)

	LENGTH	WIDTH
NIGP 116388	7.00	7.50
NIGP 116389	6.80	4.40

Remarks

In the general shape of the valve, this form appears to be similar to the type species *Bagenovia sajanica* Horný (Radugin 1937: 301, figs 5, 5a; Horný 1957: 428, pl. III, figs. 1-6) from the Early Cambrian of west-Sayan, Siberia, but differs in the presence of more numerous radiating costae and in the subcircular outline. In apical view, this species is also similar to *Bagenovia kazakhstanica* Koneva (Koneva 1976: 127, Figure 1; 1979: 22, pl. II, figs. 1-10, pl. III, figs. 1-2) from the Early Cambrian Lenian Stage of central Kazakhstan. It can be distinguished by the coarser and more numerous radiating costae, and the undulating growth lines. The most important distinguishing feature of *Bagenovia* cf. *sajanica* is that the internal structure of the valve is characterized by four pairs of asymmetrically arranged ridge-like impressions and three concentric impressions on the dorsal

valve of the cast. The internal structure of *Bagenovia kazakhstanica* possesses a longitudinal carina and more ridge-like short impressions and the presence of some small pits, especially near the apex.

Occurrence

Basal part of the Early Cambrian Xidashan Formation of Mohurshan, Kuruktag, Xinjiang and the Early Cambrian Shipai Formation of Suizhou, Hubei, China.

ACKNOWLEDGEMENTS

I wish to thank Zhang Sen-gui of the Nanjing Institute of Geology and Palaeontology, Academia Sinica for sending me the Xinjiang specimens, and K.J. McNamara, E.L. Yochelson and S. Conway Morris for reviewing the manuscript and making valuable suggestions. Thanks also to Song Zhi-yao and Mao Yong-qiang for preparing the photographs and to Ren Yu-gao and D. Hendricks for drawing the text-figures.

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First record of an Early Cretaceous theropod dinosaur bone from Western Australia

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To date the only records of dinosaurs from Western Australia have been one possible theropod bone from the Late Cretaceous (Maastrichtian) Miria Formation, south of the Exmouth Gulf, one theropod pedal phalange from the Late Cretaceous (?Turonian–Cenomanian) Molecap Greensand, and a caudal vertebra from a possible sauropod from the Middle Jurassic Colalura Sandstone of the Geraldton region (Long 1992, 1995). The only record of dinosaurs from Early Cretaceous sediments in Western Australia is from footprints preserved in the Berriasian–Valanginian Broome Sandstone exposed in the Broome region and Dampier Peninsula. This assemblage of trackways from Broome indicates a great diversity of dinosaurs existed in Western Australia at this time, ranging from theropods (Colbert and Merrilees 1967), sauropods (Thulborn *et al.* 1994), bipedal ornithischians and a possible stegosaur (Long 1993), but no skeletal remains have been recovered. Here we report the first occurrence of a dinosaur bone of Early Cretaceous age from Western Australia.

The specimen was found by one of us (JL) about 4 metres away from where a partial skeleton of a new species of the pliosaur *Leptocleidus* was found (Cruickshank and Long in press), from the Hauterivian–Barremian Birdrong Sandstone, exposed to the north of Kalbarri. It was lying on the surface scree weathered out from near the top metre of the Birdrong Sandstone, preserved in exactly the same manner as the pliosaur bones recovered from that unit. To date many such bones of pliosaurs and some ichthyosaurs have been found on outcrops of the Birdrong Sandstone, all appear to be coming out of the top metre or so of the unit. The specimen described herein was found in three pieces lying in close association, only a few centimetres apart, which were glued together to show its characteristic vertebral shape.

Description of the specimen

The specimen (WAM 96.5.1, Fig. 1) is a mid caudal vertebra. It differs from the pliosaurid

vertebrae commonly found in the Birdrong Sandstone by its much longer rostrocaudal length, narrower centrum, and its short flattened transverse processes (Fig. 1C, tr.p), and lack of subcentral foramina. The dorsal surface shows the traces of where the posterior zygapophyses were developed (Fig. 1C, po). The bone lacks the neural arch and is missing part of the posterior centrum as well as the distal face of the centrum. The anterior face of the centrum is flat, a characteristic of theropod mid caudal vertebrae, and is much larger than the estimated size of the posterior face of the centrum. In this respect it differs from the caudal vertebrae in hypsilophodontids and basal iguanodontians in general (Galton 1974, Coria and Salgado 1996). Sauropods tend to have long tails and so the mid-distal caudal vertebrae are mostly elongated, amphicoelous, with approximately equal anterior and posterior centrum faces (McIntosh 1990), unlike the Birdrong specimen. Most thyreophorans, or the armoured ankylosaurs and stegosaurs, have specialised tails bearing enlarged clubs, spines or heavy dermal ossicles, and thus the mid caudal vertebrae are more robust with strongly overlapping postzygapophyses (Coombs *et al.* 1990; Coombs and Maryanska 1990).

By comparison with the tail vertebrae of *Allosaurus fragilis* (Madsen 1976) and direct observation of other theropod dinosaur skeletons (e.g., *Gorgosaurus libratus*, W.A. Museum cast; *Tarbosaurus bataar*, Palaeontological Institut, Moscow 551– 4/49) it is most likely from a theropod. It compares very closely in overall proportions with the 37th–40th caudal vertebrae of *Allosaurus fragilis* (Madsen 1976, pl. 35 F,G,) but is about half the size, suggesting that the Birdrong theropod may have been in the order of 5 m maximum length.

Discussion

Early Cretaceous theropods thus far recovered from Australia mostly come from the Albian–Aptian Otway and Strzelecki Groups of Victoria. They include the allosaurid *Allosaurus* sp. (Molnar

et al. 1981, 1985), an ornithomimid, *Timimus hermani* (Rich and Rich 1994), a possible caenagnathid (Currie *et al.* 1996) and isolated teeth and bones of dromaeosaurids (P.V.Rich and T.H.Rich., pers. comm. 1996). Other early Cretaceous Australian theropods are *Kakuru kujani* and other isolated theropod bones from the opal fields of Andamooka, and Coober Pedy, South Australia (Molnar and Pledge 1980) as well as from Lightning Ridge in New South Wales (*Walgettosuchus*, *Rapator*; Long 1993). The Birdrong bone precludes comparison with these forms as all are known from very scant remains, often from only one bone, and all of the above mentioned taxa

do not have the caudal vertebrae preserved (except *Walgettosuchus*, which is undiagnostic as to family, Long 1993). The Birdrong specimen compares well with mid-posterior caudal vertebrae of *Allosaurus fragilis*. The bone probably represents a small tetanuran theropod of indeterminate family.

The specimen demonstrates the further potential for future discoveries of dinosaurs from this unit which outcrops extensively to the north as far as Cardabia Station (McLaughlin *et al.* 1995). To date, wherever the Birdrong Sandstone has been identified, it has yielded abundant fossilised wood and scant marine reptile remains, including the first partially articulated remains of ichthyosaurs from Western Australia, found in the northernmost exposures of the unit, collected by a WA Museum field party in July 1994. Cruickshank and Long (in press) note that the other known occurrences of the pliosaur *Leptocleidus*, which occurs in the Birdrong Sandstone, are always with an associated dinosaur fauna (e.g., eastern Cape Province, South Africa; Wealden Beds, U.K.; Coober Pedy, South Australia), further reinforcing the suggestion that the Birdrong Sandstone has great potential for future dinosaur discoveries.

ACKNOWLEDGEMENTS

We thank the financial sponsors of the 1993–1994 Birdrong expeditions, Mr John Clema of Forrestfield, and Forrestania Gold Pty Ltd, and extend thanks to various colleagues who helped in the field (Alex Baynes, Kris Brimmell, Greg Milner, Mikael Siverson, Alex Ritchie), and to the owner and managers of Murchison House Station for kindly permitting us to work on their property. We thank Kris Brimmell for photography and Danielle Hendricks for drafting Fig. 1, and also we thank Dr Ralph Molnar (Queensland Museum) and Dr Tom Rich (Museum of Victoria) for their helpful comments on the manuscript.

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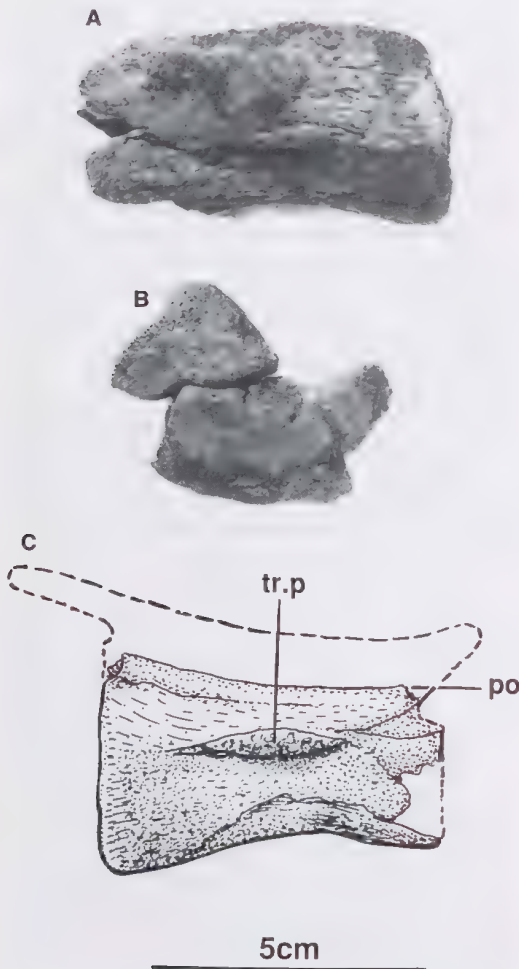


Figure 1 A, theropod mid caudal vertebra seen in right lateral view, and B, anterior view, natural size. C, Sketch of theropod mid caudal vertebra in left lateral view, showing main features, with restoration of suggested outline. Scale bar is 5 cm. Abbreviations: po, basal section of posterior zygapophysis; tr.p, transverse process.

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Manuscript received 28 August 1996; accepted 3 December 1996.

The first record of the Fiddle-back Spider *Loxosceles rufescens* (Araneae: Sicariidae) from Western Australia

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The venom of several species of *Loxosceles* (often termed Fiddle-back Spiders due to the distinctive markings on the carapace) are reported to have deleterious effects upon humans and several species are capable of forming severe necrotic lesions and occasionally death (Schenone and Suarez 1978).

These spiders, previously placed in their own family, Loxoscelidae (e.g., Gertsch 1949; Gertsch and Ennik 1983) or in the Scytodidae (e.g., Gertsch 1967), are now placed in the subfamily Loxoscelinae, in the Sicariidae (e.g. Simon 1893; Platnick *et al.* 1991). Numerous species have been described from Africa, southern Europe and the Americas, which appears to represent the full natural distribution of the genus.

Two *Loxosceles* species are reported to have been transported to various parts of the world through indirect human agency. The most widely distributed is *L. rufescens* (Dufour), a species with a natural circum-Mediterranean distribution, now reported from many other regions including U.S.A., east Asia, Australia, Madagascar, many islands of the Pacific and Atlantic (such as Hawaii) (see references in Bonnet 1957; Gertsch and Ennik 1983; Platnick 1989, 1993). The sole Australian records of this species are from Adelaide and other regions of South Australia (Gray 1974; Southcott 1976, 1978), where the species seems to have been established for some time. Southcott (1978) reported that specimens in museum collections dated back some 'forty years'.

The second is *L. laeta* (Nicolet) from western South America, which has been introduced into other areas of South and central America (e.g., Brazil, Argentina, Colombia, Ecuador and Belize), U.S.A., Canada, Australia and Finland (Gertsch and Ennik 1983). The sole Australian record was of a single male from the central city area of Sydney, New South Wales [Gray 1974; under the name *L. rufipes* (Lucas) – see Gertsch and Ennik (1983) for a clarification of this nomenclatural problem].

An examination of some spider material donated to the Western Australian Museum by Dr B.Y. Main uncovered a previously unrecognised specimen of *L. rufescens* collected in Nedlands, an

inner suburban area of Perth, in early 1957. The identification of this specimen, an adult female, was confirmed by examination of the internal genitalia which conform to that described for the species by Gertsch and Ennik (1983, figures 349–351). The specimen was found amongst packing cases which had been delivered from Singapore. However, it may well prove impossible to ascertain the exact provenance of the specimen, as the association with packing cases from Singapore may be fortuitous.

No other specimens of *Loxosceles* has been found amongst the collections of the Western Australian Museum or any similar repository (such as the Department of Agriculture, Perth), and none has ever been reported from Western Australia. Therefore, it seems likely that the species has not become established in Perth, and that the sole specimen reported here was a chance introduction.

Despite the long presence of *L. rufescens* in Australia, it seems that bites from these spiders are either very infrequent or are misdiagnosed. Sutherland (1983) reported that no bites by this spider have occurred in Australia.

Material Examined

Australia: Western Australia: 1 ♀, Nedlands, Perth, 'found amongst packing cases from Singapore', April 1957, S. Barker (WAM 96/854, BYM 1957/A8).

ACKNOWLEDGEMENTS

I wish to thank Barbara York Main for access to this specimen and for her detailed comments upon an early draft of the manuscript; Julianne Waldock for sorting the specimen from the collection; and Peter Davis for access to the Department of Agriculture collection.

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Mnuscript received 12 August; accepted 2 December 1996.

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Records of the Western Australian Museum



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Records of the Western Australian Museum

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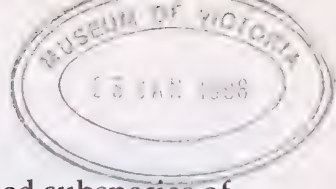
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Printed and published by the Western Australian Museum
© Western Australian Museum, November 1997
ISSN 0312 3162

Cover: The cuttlefish *Sepia apama*.
Illustration by Jill Ruse.



Chlamydera guttata carteri Mathews, 1920 – an overlooked subspecies of Western Bowerbird (Ptilonorhynchidae) from North West Cape, Western Australia

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Abstract – The subspecies of Western Bowerbird named *Chlamydera guttata carteri* Mathews 1920, known only from the North West Cape of Western Australia, has remained in the synonymy of *C. guttata* since 1930. A review of all known specimens of *C. g. carteri* and of 33 other *C. guttata* skins from adjacent areas of Western Australia indicate that *C. g. carteri* of North West Cape is a valid subspecies distinctive in its significant small size, particularly wing length, and plumage markings and coloration. Populations of nine other passerine species isolated on North West Cape, one a diminutive endemic subspecies, indicate this as a historic centre for avian subspeciation.

INTRODUCTION

Populations of spotted bowerbirds (*Chlamydera*) from the arid interior of central Australia and mid-central Western Australia were long ago considered to be sufficiently different from those of western Queensland, New South Wales and Victoria to be treated as specifically distinct and were given the name *Chlamydera guttata* by John Gould (1862). They reach the western coastal zone in the area of North West Cape and Burrup Peninsula of northwestern Western Australia (Storr 1984, Figure 1). Among other differences, they have no sign of the conspicuously contrasting nape patch of uniform grey feathering typical of the eastern form. The specific status of *C. guttata* was widely accepted until Mathews (1912, 1946) combined it with the eastern form, *C. maculata*.

Most authors subsequent to Mathews (1946) have treated all populations of Australian spotted bowerbirds as a single species under *C. maculata* (e.g., Whittell and Serventy 1948, Mayr 1962, Gilliard 1969, Schodde 1975, Storr 1977, Cooper and Forshaw 1977). Mayr and Jennings (1952) suggested the possibility, however, that what they termed the "guttata group" of bowerbirds in central and western Australia might again be considered a species separate from *C. maculata* of eastern Australia. They considered the material available to them of the *guttata* group "altogether insufficient for determination of geographical variation" and noted that study of more extensive material was desirable. Keast (1961) repeated the view that the *maculata* and *guttata* populations "were approaching, or have reached, that stage of differentiation typical of species".

Schodde (1982) subsequently acknowledged the

mid-central and Western Australian populations of spotted bowerbirds to constitute the distinct species *C. guttata* of Gould (1862). In publications too numerous to detail here, opinion as to the status of *guttata* as a good species or merely as a subspecies of *C. maculata* has swung back and forth during the past two decades. Suffice to say that while the influential ornithological works of Mayr and Jennings (1952), Gilliard (1969), Hall (1974), Schodde (1975), Cooper and Forshaw (1977), Storr (1984, 1985, 1991) treat *guttata* as only a subspecies of *C. maculata*, more recent works accept *C. guttata* as a full species (Schodde and Tidemann 1986, Sibley and Monroe 1993, Christidis and Boles 1994). Little is published supporting either action. Populations of *C. guttata* have now come to be known collectively as the Western Bowerbird.

Based on a specimen (sex not indicated) collected at "North-west Cape, Mid-west Australia, August 7th, 1916", Gregory Mathews (1920) named a new subspecies of spotted bowerbird *Chlamydera maculata nova*. In describing this new subspecies Mathews wrote that it "Differs from *C. m. subguttata* Mathews in having the yellow on the breast and abdomen much deeper and richer flank markings bolder, less black on the throat and upper chest, and the bill smaller" but did not present measurements of birds. The subspecies *C. m. subguttata* Mathews, 1912 was described from the East Murchison River, near Wiluna in Western Australia (see Figure 1), but was subsequently treated as invalid by Mathews himself (Mathews 1930, 1931) and by all subsequent authors.

Within three months of erecting the name *C. m. nova*, Mathews found that it was preoccupied and renamed it *C. m. carteri*, after the original collector

Tom Carter (*in* Carter and Mathews 1920). This subsequent publication contains a brief but slightly expanded description of *C. m. carteri*, and is accompanied by a colour plate of the specimen collected on 9 August 1916 and now in The Natural History Museum, Tring (BMNH 1931.8.1.1). In the plate the lilac nuchal crest is shown to be far larger than it actually is in The Natural History Museum specimen or in any specimens of *carteri*. This may have led Iredale (1950) to state erroneously of *C. m. (nova) carteri* that "The female has a large nuchal frill". Carter and Mathews (1920) also stated that about half the nuchal crest feathers of the only male collected were deep golden yellow but these are in fact simply some crest feathers with a rose-reddish hue, which also occur, to a lesser extent, in the female H. L. White (HLW) specimen 6591 in the Museum of Victoria. The text also refers to a series of six birds obtained at North West Cape; a seventh specimen detailed herein was collected by Gerlof Mees in 1959. Tom Carter published some

notes on the Cape Spotted Bower-bird (still as *C. m. nova*), stating that he had first collected a specimen of it in February 1892 (Carter and Mathews 1921). The specimen unfortunately reached Melbourne as a "mass of loose feathers" (Carter 1903, Carter and Mathews 1921) and has apparently not survived to the present day.

By the time Mathews published the second part of his *Systema Avium Australasianarum* (Mathews 1930), he had apparently lost confidence in the validity of *C. m. carteri* and consigned it to the synonymy of *C. m. guttata*. In a comprehensive review of Australian bowerbirds to subspecific level, Mayr and Jennings (1952) treated the Mathewsian subspecies *nova*, *subguttata* and *macdonaldi* (the last referring to birds of the Macdonnell Ranges, Central Australia) as synonyms of *C. m. guttata*. This conclusion, however, was presumably based upon examination of only the single specimen of *carteri* in the American Museum of Natural History (AMNH). Since that time *C. guttata carteri* has remained unrecognised (Marshall 1954, Serventy and Whittell 1962, Gilliard 1969, Cooper and Forshaw 1977, Storr 1984, Ford 1987a).

Recent field studies of Western Bowerbirds on North West Cape proved the species to be a common breeding resident, with bowers of males and nests of females not difficult to find (Serventy 1955, Kolichis 1979, Bradley 1987).

METHODS

We examined the three North West Cape specimens of *C. guttata*, from the H. L. White (HLW) collection in the Museum of Victoria and found them to be conspicuously different from birds from the Hamersley Range and the East Murchison River area (see Figures 1 and 2). The northwest end of Hamersley Range is not as discrete as indicated in Figure 1, but becomes lower and broken towards Onslow. During a more recent study tour of most world bird collections containing significant numbers of birds of paradise (Paradisaeidae), we also took the opportunity to examine all available specimens of *C. guttata* from the North West Cape and adjacent areas of Western Australia (see Table 1). In addition to the H. L. White specimens from North West Cape, one was examined in the The Natural History Museum, Tring, two from the Western Australian Museum, Tring, and one at the American Museum of Natural History. Measurements of skins were taken in the standard way. The wing was measured straightened and flattened, with a stopped rule; tail length was taken from the point of insertion of the central pair of feathers into the skin to the tip of the longest feather; and bill width was taken at the anterior margin of the nostril with

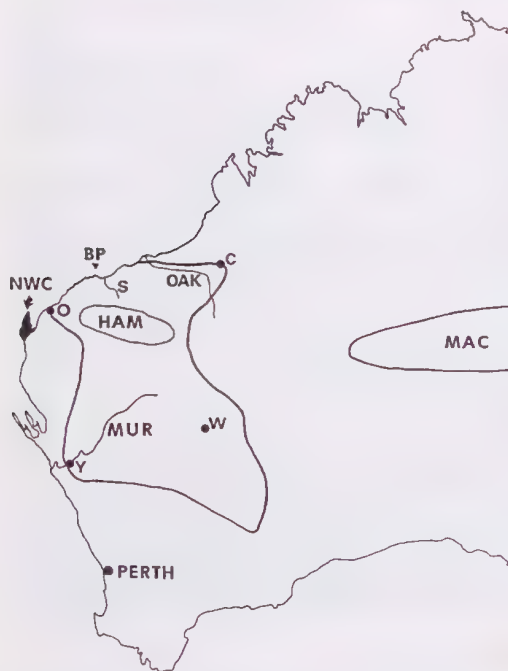


Figure 1 Map of western continental Australia showing locations mentioned in the text or Table 1. Solid black area = North West Cape (NWC); C = Callawa; HAM = Hamersley Range; MAC = Macdonnell Range; MUR = Murchison River; O = Onslow; BP = Burrup Peninsula; Oak = Oakover River; S = Sherlock River; W = Wiluna; Y = Yandil. The solid line encompassing Onslow and the Hamersley and Murchison areas and that encompassing and extending west of the Macdonnell Range indicates the approximate range of *C. guttata* in Western Australia.

digital calipers. Observed differences in some of the measured characters between paired populations of birds were tested for levels of significance with Student's *t*-test. All skins of *C. guttata carteri* and several other skins of *C. guttata* from locations about the North West Cape area in various museums (see Table 1) were photographed under equivalent conditions to enable comparison.

RESULTS

As the morphology of the three North West Cape specimens of *C. guttata* in the Museum of Victoria collection (HLW 6590, 6591, 6592) and the two in the WAM (A8713 collected by Mees and A1224 collected by Carter) was the same (and like that of the two North West Cape specimens examined elsewhere), we first present a composite description of these, with comparative reference to some other *C. guttata* specimens held in the Museum of Victoria. Following this, we briefly comment on the two North West Cape specimens held outside Australia:

The five North West Cape birds held in Australian collections differ conspicuously from those of the Hamersley Range and the East Murchison River area. In the North West Cape birds, the chestnut spotting of the blackish nape

(below the pink nuchal crest) is finer and denser than in birds to the immediate east and south-east. The chestnut spotting on the lower mantle, back, rump and upper tail coverts is also denser (ie. there is less black). The pale spots on the mantle of the North West Cape birds typically have the converging straight edges of the upper half meeting in a sharp point at their apex. This is in marked contrast to those of birds to the south and south-east, in which these spots are typically rounded about their upper half as well as the lower, the spots being roughly circular or heart-shaped overall. Moreover, in North West Cape birds the back spotting is uniformly chestnut, whereas in the adjacent populations the colour of back spotting is variable (chestnut to buff).

The crown of North West Cape birds is conspicuously different from that of birds found to the east and the southeast in being much more finely spotted (almost streaked on the forecrown) chestnut, the black edge of the individual feathers being much finer. The result is that the crown in North West Cape birds is overall more uniformly chestnut than the more variegated and more heavily black-marked crowns in adjacent populations. There is no silver tipping to the crown feathers as is typical of specimens of *C. guttata* to the east and southeast. Ear coverts and throat



A

B

Figure 2 Dorsal (A) and ventral (B) views of Museum of Victoria specimens of *Chlamydera guttata* from Western Australia: three being of *C. g. carteri* from the North West Cape (upper left), four of *C. g. guttata* from the Hamersley Range (upper right), and four *C. g. guttata* from the east Murchison River (lower).

feathers, and those of the upper breast, have far less extensive black edges than in birds to the south and the southeast. This gives these parts of the bird a far more uniformly chestnut look (as in the crown) than the much blacker appearance of these parts in birds from the Pilbara and Murchison (Figure 2).

The 'blackish' colour in the wings (primaries and secondaries) and upper tail (notably the central pair of rectrices) is less black, tending more to brown, in the North West Cape birds than in those to the east and southeast. This is a slight but nevertheless consistent difference found in all five North West Cape birds. The pale broad edging to the primary and secondary wing coverts in four of the North West Cape birds is similar in colour to those in adjacent areas but in Museum of Victoria female skin HLW 6591, it is rich chestnut, as is the back spotting of all five North West Cape birds.

The rich chestnut of the sides of the breast, flanks and thighs is most noticeably more extensive in North West Cape birds than in those to the east and southeast. In birds from the latter areas the chestnut is confined more to the sides of the abdomen, the flanks and the thighs, where the colour is less intense. In North West Cape birds the rich chestnut extends all the way up the sides and further out onto the sides of the flanks, abdomen and breast than in the other birds (in which it is mostly concealed by the wings), and this joins the chestnut of the throat and sides of the neck. The

only exception to this is a crestless female specimen in the WAM (A4126) from Yandil Station on the West Murchison River which has rich and extensive chestnut similar to the North West Cape birds. It shows no yellow on its underparts, however, and has the crown, mantle and back plumage of the East Murchison birds while its chin and throat feathering is somewhat intermediate in coloration and marking. Thus, while it does exhibit the rich extensive chestnut otherwise found only in North West Cape birds, it lacks the yellow underparts of North West Cape birds. Its upperparts are as in East Murchison birds and it is significantly and exclusively larger than North West Cape birds in all but bill length (= 29.7 mm, the length of the shortest-billed North West Cape bird). Thus, the Yandil bird is an atypical Murchison River area individual that is clearly not associated with the geographically remote (Figure 1) and distinctive North West Cape birds.

The specimen of *C. guttata carteri* in the AMNH (679152) collected by Carter at Hooroomooroo, North West Cape on 6 August 1916, has the same appearance as the above North West Cape specimens, with the extensive chestnut thighs, flanks and sides of the breast. The throat is similarly more buff and less black as in other North West Cape birds, but unlike one from Onslow and those from other adjacent areas in the AMNH collection. The crown feathers of the AMNH specimen are streaked and spotted dark chestnut with fine black outer edging and lack silvery tips; the nuchal crest is small. In comparison the bird from Onslow (AMNH 679153) has the crown only spotted dark chestnut, with much silver tipping to the feathers; the nuchal crest is large. The Onslow bird has far less extensive chestnut on its flanks than the North West Cape birds. A bird from 10 miles north of Tambrey, Sherlock River, which is directly north of the central Hamersley Range, is similar to the Onslow specimen. Thus the Onslow and Sherlock River birds are unlike the North West Cape birds but are like those from Hamersley Range.

The single specimen (1931.8.1.1) of *carteri* in the BMNH was collected by Carter on 9 August 1916 at North West Cape. In general markings and coloration it is extremely similar to the specimen in the AMNH and, while its nuchal crest is slightly larger than in North West Cape skins in the Museum of Victoria and AMNH, it is conspicuously smaller than in birds from Onslow, Sherlock River, Hamersley Range and East Murchison area.

Table 1 summarises the measurements of the seven North West Cape specimens and of an additional 33 *C. guttata* skins from adjacent areas held at various museums. Wing and tail lengths of the birds of the Hamersley and Murchison areas

Table 1 Mean measurements (boldface), standard deviations and sample sizes for 40 Western Bowerbird *Chlamydera guttata* specimens¹ from North West Cape (*C. g. carteri*), Hamersley Range and Murchison River area (*C. g. guttata*) of Western Australia.

	Wing length	Tail length	Tarsus length	Bill length	Bill width	Total head length
North West Cape ²	137	91	36.6	30.2	7.6	57.1
	2.77	3.19	0.61	1.00	0.43	-
	7	7	7	7	7	1
Hamersley Range ³	149	94	38.4	30.6	7.4	58.4
	1.27	9.96	1.37	0.78	0.44	1.09
	13	12	13	13	13	12
Murchison River ⁴	148	95	38.9	30.4	7.5	58.0
	2.31	5.35	1.15	1.20	0.32	1.07
	20	20	20	20	20	19

¹ 12 from Museum of Victoria, 11 Western Australian Museum, 10 National Wildlife Collection, CSIRO, 5 American Museum of Natural History, 1 South Australia Museum and 1 The Natural History Museum, Tring.

² 6 females and 1 adult male.

³ 7 adult males, 2 subadult males and 4 females (including 1 from Onslow, 1 from Oakover River, 1 from Callawa and 1 from the Sherlock River – see Figure 1).

⁴ 11 adult males, 2 subadult males and 7 females.

are almost identical (Table 1), there being no significance between them ($t = 1.119$, $P > 0.1$ and $t = 0.163$, $P > 0.1$ respectively). The wing and tail length of North West Cape birds are much shorter than those of birds from the Hamersley Range immediately to the east, however, and the differences are significant ($t = 10.417$, $P < 0.001$ and $t = 2.089$, $P = 0.05$ respectively). Differences in wing and tail lengths of the North West Cape birds compared with those of both the Hamersley and Murchison areas combined (Table 1, Figure 1) are also significant ($t = 10.072$, $P < 0.001$ and $t = 2.471$, $P < 0.02$ respectively).

DISCUSSION

We agree with the current view that there is no justification for taxonomically distinguishing between populations of *C. guttata* of the Hamersley Range and Murchison River areas (Figure 2). Birds from the former may be on average slightly more brownish in the throat and darker on the crown; however Museum of Victoria specimens HLW 6772 and 6774 (subadult and adult male respectively) from the Hamersley Range are all but identical to specimens HLW 1137 and 1138 (subadult and adult male respectively) from the East Murchison in throat, crown, upperparts and all other plumage. Measurements of birds from these two areas are similar (Table 1) and show no significant difference. We do note that a number of species show geographic variation between west and east Murchison (R. E. Johnstone *in litt.*).

It is clear from results presented in Table 1 and above that the seven birds from the North West Cape of Western Australia are on average significantly smaller than those from the adjacent Hamersley Range area (including Onslow and Sherlock River) in wing length (8%) and, to lesser extent, tail (4%) and tarsal length (5% shorter), while their bills are only fractionally smaller and therefore are disproportionately long and broad relative to overall body size. Inexplicably, the original description of *C. g. carteri* (Mathews 1920) includes the statement "and the bill smaller [than *C. m. subguttata*]", and a subsequent description (Carter and Mathews 1920) stated that the "bill of this new subspecies is distinctly smaller, and about 5 mm shorter [than in *C. m. subguttata*]".

The lilac nuchal crest feathers of the North West Cape birds are all far shorter than those of birds from elsewhere, and the crest thus forms a far narrower band. They were not measured, but the shorter crest is nevertheless clearly apparent (Figure 2). The crown coloration and markings of birds from North West Cape differ obviously from those on birds of adjacent areas. This is significant because speciation in bowerbirds is typically emphasized by marked differences in crown

colour. Examples of this are differences between the catbirds *Ailuroedus crassirostris* and *A. melanotis* within Australia and between subspecies of *A. buccoides* and of *Chlamydera lauterbachii* in New Guinea. Likewise, crest size differences among the gardener bowerbirds, *Amblyornis*, of New Guinea reflect speciation in this genus (Gilliard 1969, Schodde and McKean 1973, Frith and Frith *in press*). These examples support the argument that the population of *C. guttata* that is apparently confined to the North West Cape area (Blakers *et al.* 1984, Storr 1984, Ford 1987a, Kendrick 1993) has differentiated at least subspecifically.

The degree of morphological differentiation of *C. guttata carteri* from conspecifics to the east and southeast is far greater than that between the populations of the Hamersley Range and on the Murchison River (see above, Table 1, Figure 1) to which Schodde (in Schodde and Tidemann 1986) was alluding when indicating the species to consist of "one or two races" (Schodde *in litt.*). It is greater than the difference between the far more extensively distributed, mid-central and mid-western Australian populations of *C. guttata*. The difference between *C. g. carteri* and *C. g. guttata* is not unlike the degree of differences found between the long and presently recognised subspecies within *C. nuchalis* and *C. lauterbachii* (Gilliard 1969, Cooper and Forshaw 1977), notwithstanding that Schodde (in Sibley and Monroe 1990) doubted the validity of subspeciation within the latter species.

In view of the above, *C. guttata carteri* Mathews of the North West Cape should be recognised as a subspecies until such time as further collecting and/or genetic studies demonstrate otherwise. Storr (1986), Blakers *et al.* (1984) and Kendrick (1993) clearly indicated the isolated nature of the North West Cape bowerbird population. That its geographical range is so limited is of considerable interest on a continent where this is rarely the case for avian taxa at any level (Keast 1961). Storr (1984) noted ten bird species (one non-passerine and nine passerines) with populations isolated on the Cape Range of the North West Cape. In acknowledging and discussing the Cape Range as a minor geographical isolate, Ford (1987a) noted it is separated from rangelands in the Pilbara by a water barrier (Exmouth Gulf) and a lowland vegetated with open scrub steppe. Ford (1987b) shortly thereafter named the isolated population of Grey Shrike-thrush on the Cape Range of North West Cape as the diminutive subspecies *Colluricincla harmonica kolichisi*.

Because the female AMNH 679152 specimen is dated 6 August 1916, it clearly cannot be the type of *C. maculata nova* designated by Mathews (1920), as he specified in his description a female collected on "August 7th, 1916". Thus the type must be one of the two females collected on 7 August and now

in the Museum of Victoria, Melbourne (NMV, HLW 6590 and 6591). The International Commission for Zoological Nomenclature recommends that, in the case of such a situation in a revision of a taxon (such as the present one) a lectotype be formally designated. We therefore designate the Museum of Victoria female specimen NMV, HLW 6591 as the lectotype of *Chlamydera guttata carteri*. This specimen was collected on 7 August 1916 and has "nova type" written in pencil on Tom Carter's original label. The other five specimens of this form collected during early August 1916 are therefore paralectotypes.

For bibliographical comprehensiveness and in order to avoid potential future confusion, we note that in his account of his collection of the type series of *C. g. carteri*, Carter (in Carter and Mathews 1921) provided chronological details contrary to the label data on his specimens. His account indicated that he collected four birds on 6 August, another on 7 August and one more on 9 August 1916. As label data on Carter's female specimens are unambiguously clear, we use these and conclude that his subsequent written account is erroneous.

A possible additional factor contributing to the isolation of *C. g. carteri* on the North West Cape is, as several authors have noted, that Western Bowerbirds feed a great deal upon fruits of, and thereby closely associated with the distribution of, the fig tree *Ficus platypoda*, which grows in sheltered woodland among rocky ranges (Marshall 1954, Serventy 1955, Serventy and Whittell 1962, Gilliard 1969, Cooper and Forshaw 1977, Binsted 1978). This rock-associated fig is significantly sparse or absent in the expansive low arid desert sand plains that separate the sandstone and limestone Cape Range of the North West Cape from more extensive and complex rocky outcrops of the Hamersley Range to the east (CSIRO 1960). Emphasizing the significance of the (approximately two hundred kilometre) isolation of the (up to 300 metres above sea level) dissected limestone ranges of the Cape Range is that the skink *Lerista allochira* is a distinct species dependant upon and endemic to them (Kendrick 1989). In addition, four other reptiles species are all but endemic to the Cape Range peninsula in that three occur elsewhere only to a short distance eastward and one a short distance southward (Kendrick 1993). The lack of available water in this arid lowland barrier might also be significant. If so, these factors would account for the isolation and resultant marked differentiation of the North West Cape Western Bowerbird population (Figure 1, Table 1, Plate 1). The fact that *C. guttata* has spread, probably only quite recently, beyond the southern limit of *Ficus platypoda* (R. E. Johnstone *in litt.*) does not negate this possibility.

ACKNOWLEDGEMENTS

This study would not have been possible without the cooperation of several institutions and their staff. We acknowledge Peter Arnold, Museum of Tropical Queensland, Les Christidis, Ian McAllan and Rory O'Brien, Museum of Victoria, Melbourne; Richard Schodde, Ian Mason and John Calaby, National Wildlife Collection, CSIRO, Canberra; Ron Johnstone, Western Australian Museum, Perth; Lester Short, Joel Cracraft, Mary LeCroy and the Chapman Fund, American Museum of Natural History, New York; Philippa Horton, South Australian Museum, Adelaide and Robert Prys-Jones, Peter Coulston and Michael Walters, The Natural History Museum, Tring, U.K. for access to and/or help with specimen loans or literature. Joan Airey, Jeff and Barbara Davies, Peter and Daphne Fullager, Mary LeCroy and Peter and Janet Marsack provided most kind hospitality. For constructively commenting on a draft of this contribution we sincerely thank Walter Boles, Allan Burbidge, Les Christidis, John Dell, Ron Johnstone, Norbert Lenz, Ian McAllan and Richard Schodde. Dedicated to the memory of Dom. (D.L.) Serventy who ruefully wrote (1950) "After the exacting task of delimiting subspecies it will be mostly a matter of selecting one of the numerous Mathewsian labels".

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Australian water mites of the genus *Arrenurus*, with the description of twelve new species from northern and western Australia (Acari: Hydrachnellae: Arrenuridae)

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Abstract – Two new subgenera of the genus *Arrenurus*, viz., *Dividuracarus* (type species *Arrenurus* (*Dividuracarus*) *tripartitus* sp. nov.) and *Brevicaudaturus* (type species *Arrenurus* *lohmanni* Piersig, 1898), and 12 new species, viz., *A.* (*A.*) *ensifer*, *A.* (*A.*) *harveyi*, *A.* (*A.*) *liliaceus*, *A.* (*A.*) *mantonensis*, *A.* (*Dividuracarus*) *gereckei*, *A.* (*Dividuracarus*) *tripartitus*, *A.* (*Megaluracarus*) *caeruleus*, *A.* (*Megaluracarus*) *gilvovs*, *A.* (*Micruracarus*) *anbangbang*, *A.* (*Micruracarus*) *jibiruensis*, *A.* (*Micruracarus*) *purpureus* and *A.* (*Micruracarus*) *separatus* are described from Northern Territory and Western Australia. Further, a description is provided for the females of *A.* (*Brevicaudaturus*) *lohmanni* Piersig, *A.* (*A.*) *balladoniensis* Halík and *A.* (*Megaluracarus*) *vanderpalae* Smit, while a more detailed description is given for *A.* (*Megaluracarus*) *thienemanni* K.O. Viets. In addition, three species are reported new for the fauna of Australia. A key is given for the Australian species of the genus *Arrenurus*.

INTRODUCTION

Two genera of the water mite family Arrenuridae have been reported from Australia, *Wuria* and *Arrenurus*. Although the genus *Arrenurus* has a cosmopolitan distribution and is one of the most species-rich in the water mites, not more than 20 species and subspecies have been reported from Australia (see Table 1). These species belong to the subgenera *Arrenurus*, *Megaluracarus*, *Micruracarus* and *Truncaturus*. Only one species of *Wuria*, *W. boutit*, is known (Harvey 1989).

On a trip through the Northern Territory and Western Australia, areas seldom visited by acarologists, I collected 15 *Arrenurus* species new for the fauna of Australia, of which 12 species are new to science. Further, two new subgenera of this genus are described. A number of females of previously known species are described for the first time, and three species new to the Australian fauna are reported, i.e. *Arrenurus gracilipes* Piersig, *A. lohmanni* Piersig and *A. rouxi* Walter.

Separate keys are given for the males and females of the Australian members of the genus *Arrenurus*.

All material has been collected by the author. Western Australia and Northern Territory holotypes and paratypes have been deposited in the Western Australian Museum (Perth) (WAM), and in Northern Territory Museum (Darwin) (NTM) respectively. Further, paratypes and almost all non-type material have been deposited in the

Zoological Museum of the University of Amsterdam (ZMA).

The following abbreviations have been used (see Figure 9): L1–4 lateroglandularia 1–4; A1–2 pre- and post-antennal glandularia; D1–4 dorsoglandularia 1–4; CX1–4 coxal plates 1–4; PI–PV palp segments 1–5; l.p. ligulate process; SMF – Forschungsinstitut und Naturmuseum Senckenberg. All measurements are in μm , measurements of leg and palp segments are of the dorsal margins. Measurements of paratypes in the description of new species are given in brackets. Unless otherwise stated, all species have the second, third and fourth legs with numerous swimming setae

SYSTEMATICS

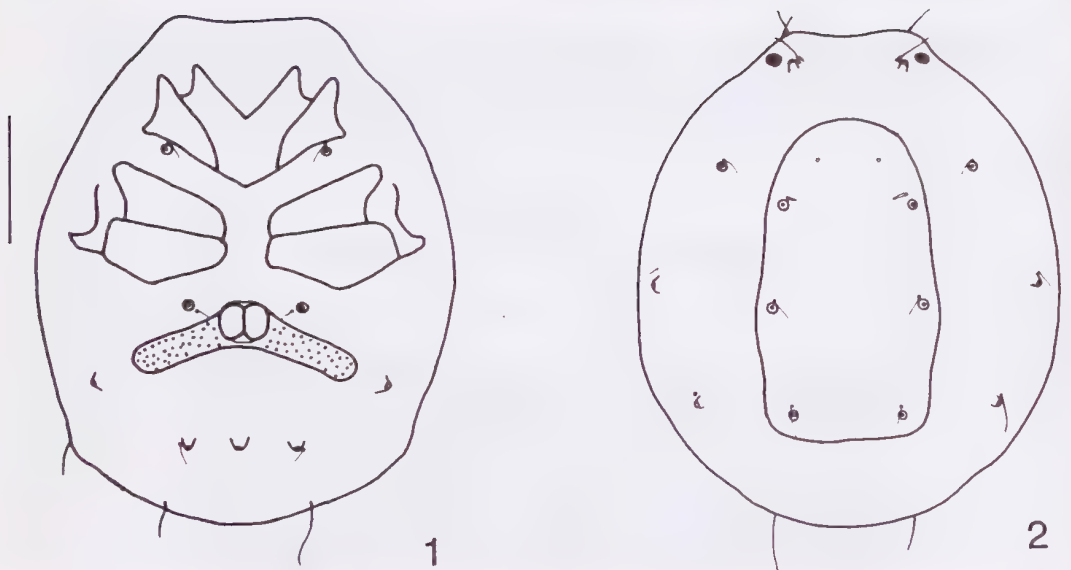
Arrenurus (*Arrenurus*) *balladoniensis* Halík Figures 1–2

Arrenurus balladoniensis Halík, 1940: 283; Halík, 1941: 106; Cook, 1986: 305; Smit, 1992: 106.

Arrenurus quadripapillatus Lundblad, 1941: 120; Lundblad, 1947: 74.

Material Examined

Australia: Northern Territory: 13 ♂, 13 ♀, ponds in Ormiston Creek, Ormiston National Park, 6 August 1994 (ZMA). **Western Australia:** 2 ♂, 2 ♀, Lake Monger, Perth, 26 August 1994 (ZMA).



Figures 1-2 *Arrenurus (Arrenurus) balladoniensis* Halik, ♀: 1, ventral view; 2, dorsal view. Scale lines, 500 µm.

Description

Female

Body 1944 (1848–2232) long and 1656 (1656–1932) wide. Body colour yellow. Anterior body margin slightly concave. Posterolateral corners of body absent. Dorsal shield slender (Figure 2), rounded anteriorly, truncated posteriorly; dorsal shield 1272 long and 708 wide. Capitular bay V-shaped. Distance of CX4 about two times width of one genital valve. Medial margin of CX3 and CX4 of equal length. Gonopore 175 long. Genital valves with small chitinous patches. Genital plates straight and narrow, sloping posteriorly, slightly widened laterally (Figure 1). Lengths of PI–PV: 55, 137, 115, 156, 92; PII with two setae on medial side. Lengths of I-leg-4-6: 243, 223, 223. Lengths of IV-leg-4-6 310, 291, 252.

Remarks

A widespread species in Australia, known from Western Australia, Victoria and Queensland. Only the male of this species was known hitherto, a description of the female is given above.

The shape of the dorsal shield of the female is similar to that of *A. fissipetiolatus* Lundblad and *A. ensifer* sp. nov.

Arrenurus (Arrenurus) ensifer sp. nov.

Figures 3-8

Material Examined

Holotype

♂, pool, Joffre Gorge, Hamersley Range National

Park, Western Australia, Australia, 13 August 1994 (WAM).

Paratypes

Australia: Western Australia: 1 ♂ (not fully sclerotized) (ZMA), 1 ♀ (WAM) and 1 nymph (?) (ZMA), Ashburton River at crossing with North West Coastal Highway, 18 August 1994.

Diagnosis

Petiole sword-like, dorsal shield of male truncated. Dorsal shield of female slender, D1 and L4 on humps.

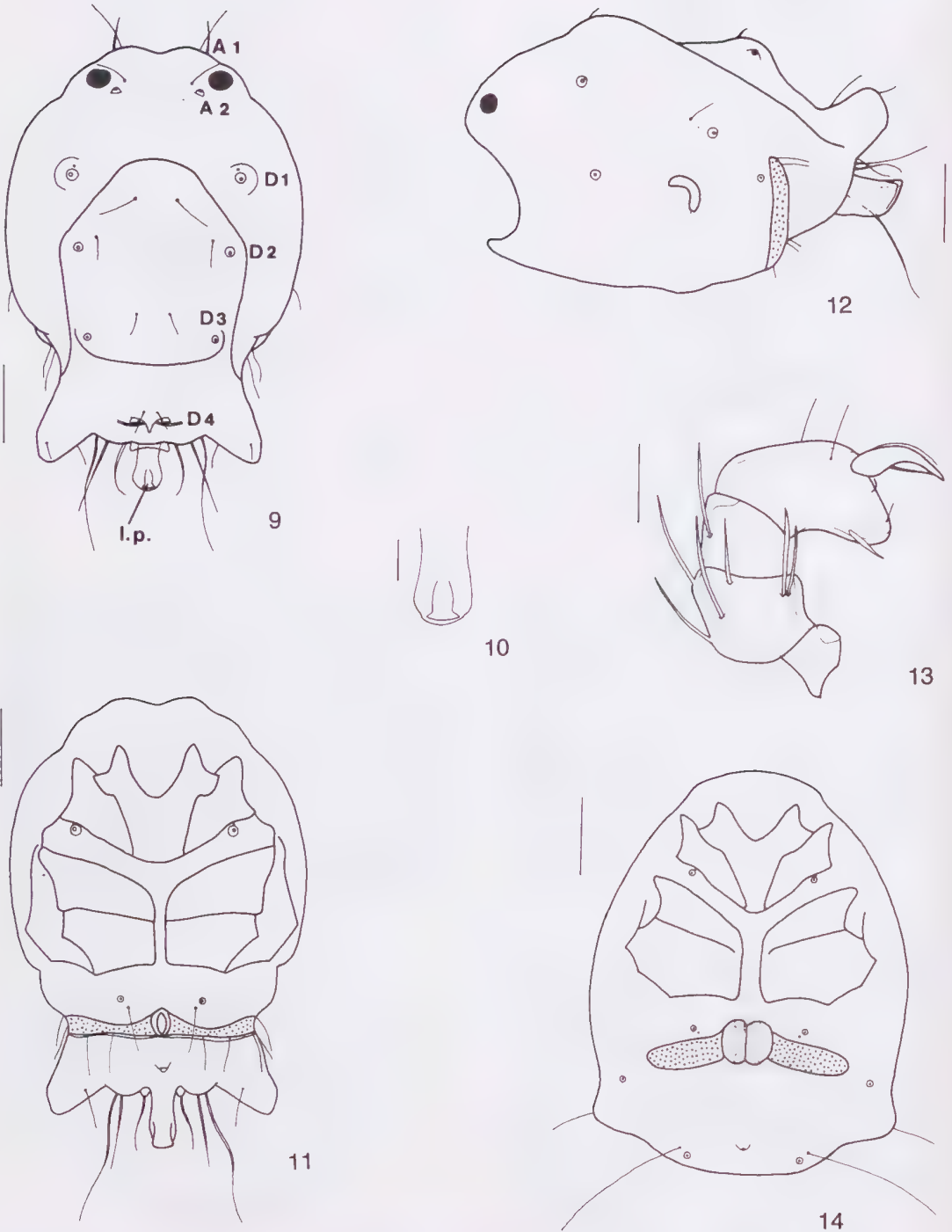
Description

Male

Body 1280 long (including petiole) and 1038 wide. Body colour yellowish. Anterior body margin concave. Dorsal shield 713 long and 446 wide, tapering posteriorly, truncated (Figure 3). D1 on large humps (Figure 5). Cauda short, almost absent. Pygal lobes well developed, broad and rounded. Hyaline membrane large. Gonopore 68 long. Genital plates not extending to lateral body margin, widened medially (Figure 4). Petiole sword-like, 232 long (measured from ventral view). Ligulate process absent. Curved setae extending to posterior margin of petiole. Lengths of PI–PV: 43, 130, 108, 130, 86; PII with 2 heavy setae on medial side near anterior margin of segment; PIV with an angular anteroventral corner. Paratype male with 4 setae on medial side of PII, of which 2 near anteroventral corner of segment. Lengths of I-leg-



Figures 3–8 *Arrenurus (Arrenurus) ensifer* sp. nov., holotype ♂ (unless stated otherwise): 3, ventral view; 4, dorsal view; 5, lateral view; paratype ♀; 6, ventral view; 7, dorsal view; 8, palp. Scale lines, 50 µm (Figure 8), 200 µm (Figures 3–6), 500 µm (Figure 7).



Figures 9–14 *Arrenurus (Arrenurus) harveyi* sp. nov., holotype ♂ (unless stated otherwise): 9, dorsal view (for explanation of abbreviations see Introduction); 10, detail of petiole; 11, ventral view; 12, lateral view; 13, palp; 14, ventral view, paratype ♀. Scale lines, 50 µm (Figure 10, 13), 200 µm (Figures 9, 11, 12, 14).

4–6: 223, 204, 213. Lengths of IV-leg-4-6: 296, 175, 194; IV-leg-4 with a short spur.

Female

Body 1416 long and 1296 wide. Anterior and posterior body margin concave. D1 and L4 on humps. Dorsal shield slender, rounded anteriorly and truncated posteriorly (Figure 7). Medial margin of CX4 longer than medial margin of CX3. Distance of CX4 larger than one genital valve. Gonopore 145 long, genital valves with small chitinous patches. Genital plates narrow and short, slightly bowed (Figure 6). Excretory pore surrounded by a large sclerotization. Lengths of PI–PV: 48, 113, 98, 124, 82; palp as in male, but PII has in anteroventral corner two large and one small seta (Figure 8). Lengths of I-leg-4-6: 213, 204, 204; lengths of IV-leg-4-6: 272, 233, 243.

Remarks

The female of the new species has a similar dorsal shield as *A. balladoniensis*, but is smaller, with distinct humps on the dorsum. Males of the two species differ in the shape of the petiole. The shape of the petiole separates the male from other species.

Etymology

The species is named after the sword-like petiole.

Arrenurus (Arrenurus) harveyi sp. nov.

Figures 9–14

Material Examined

Holotype

♂, Chinderwariner Pool, Millstream-Chichester National Park, Western Australia, Australia, 15 August 1994 (WAM).

Paratypes

Australia: Western Australia: 2 ♂ (ZMA), 1 ♀ (WAM), same data as holotype.

Diagnosis

Petiole of rounded shape, ligulate process reversed mushroom-shaped. Female with distinct posterolateral corners of the body; genital plates straight and narrow, slightly sloping; genital valves with small, rounded chitinous patches, connected by a small strip.

Description

Male

Body 1154 (1096–1135) long (including petiole) and 766 (732–745) wide. Body colour blueish. Anterior margin of body concave. Cauda and

pygal lobes well developed (Figure 9). Dorsal shield incomplete, anterior part more or less triangular. D1 on small hump; D3 on large fused, obtuse hump (Figure 12). Gonopore 49 long. Genital plates narrow and long, extending onto lateral sides of body (Figure 11). Hyaline membrane well developed, trapezoid, posterior margin concave. Petiole 146 long (measured from ventral view), extending beyond pygal lobes, rounded posteriorly. Ligulate process reversed mushroom-shaped (Figure 10). Curved setae extending to posterior margin of petiole. Lengths of PI–PV: 36, 77, 60, 96, 58; PII with 4 seta on medial side, of which 2 setae in anteroventral corner (Figure 13). Lengths of I-leg-4-6: 155, 146, 204; lengths of IV-leg-4-6: 286, 107, 146; IV-leg-4 with a spur.

Female

Body 1038 long and 825 wide. Anterior body margin rounded. Posterolateral corners very distinct. L3 on small humps. Gonopore 87 long; genital valves with small, rounded chitinous patches; anterior and posterior patch connected by a small strip. Genital fields straight and narrow, slightly sloping, laterally rounded (Figure 14). Length of PI–PV: 29, 67, 50, 88, 49. PII with 2 setae on medial side, of which one seta located anteroventrally. Length of I-leg-4-6: 87, 68, 145; length of IV-leg-4-6 175, 145, 136.

Remarks

The assignment of the female is somewhat uncertain, as two different *Arrenurus* species

Table 1. Previously reported *Arrenurus* species from Australia (compiled from Cook 1986; K.O. Viets 1975; K.O. Viets 1981; Smit 1992; Smith and Harvey 1989).

<i>Arrenurus (Arrenurus) australicus</i> Lundblad 1941
<i>A. (Arrenurus) balladoniensis</i> Halík 1940
<i>A. (Arrenurus) fissipetiolatus</i> Lundblad 1947
<i>A. (Arrenurus) pseudoaffinis</i> Piersig 1906
<i>A. (Megaluracarus) cheetus</i> Cook 1986
<i>A. (Megaluracarus) harpagopalpus</i> Walter 1929
<i>A. (Megaluracarus) margatellus</i> Cook 1986
<i>A. (Megaluracarus) otodus</i> Cook 1986
<i>A. (Megaluracarus) roobeeki</i> Smit 1992
<i>A. (Megaluracarus) rostratus</i> Daday 1898
<i>A. (Megaluracarus) rostratus degeneratus</i> K.O. Viets 1984
<i>A. (Megaluracarus) thienemanni</i> K.O. Viets 1984
<i>A. (Megaluracarus) tricornutus</i> K. Viets 1955
<i>A. (Megaluracarus) vanderpalae</i> Smit 1992
<i>A. (Megaluracarus) victorianus</i> K.O. Viets 1978
<i>A. (Micruracarus) forpicatoides</i> Lundblad 1941
<i>A. (?Micruracarus) kitchingi</i> Smith and Harvey 1989
<i>A. (Truncaturus) haswelli</i> Cook 1986
<i>A. (Truncaturus) novaeollandiae</i> Lundblad 1947
<i>A. (Truncaturus) tasmanicus</i> Lundblad 1941



Figures 15–19 *Arrenurus (Arrenurus) liliaceus* sp. nov., holotype ♂ (unless stated otherwise): 15, ventral view; 16, dorsal view; 17, lateral view; 18, palp; 19, ventral view, paratype ♀. Scale lines, 50 µm (Figure 18), 200 µm (Figures 15–17, 19).

occurred at the type locality, both represented by one female. I assigned the small female to *A. harveyi*, the large female to *A. liliaceus* sp. nov., because the male of *liliaceus* is larger than *harveyi*. The female of *A. harveyi* is close to *A. liliaceus* and *A. pseudoaffinis* and differs only in the shape of the chitinized patches of the genital valve. The shape of the ligulate process separates the male from other species.

Etymology

The species is named after Dr M.S. Harvey.

Arrenurus (Arrenurus) liliaceus sp. nov.

Figures 15–19

Material Examined

Holotype

♂, Chinderwariner Pool, Millstream-Chichester National Park, Western Australia, Australia, 15 August 1994 (WAM).

Paratype

Australia: Western Australia: 1 ♀, same data as holotype (WAM).

Diagnosis

Male with a broad, posteriorly rounded petiole; ligulate process absent; hyaline membrane large but thin, indented laterally and posteriorly. Females with distinct posterolateral corners of the body, genital valves with chitinous patches, anterior patch triangular, posterior rounded; genital plates straight and narrow, laterally widened.

Description

Male

Body 1242 long and 883 wide. Body colour blueish-green. Anterior margin of body concave. Cauda and pygal lobes well developed. Dorsal furrow incomplete (Figure 16). D1 and D4 on humps (Figure 17). Gonopore 65 long. Genital plates long, wing-shaped, not extending to lateral body margin (Figure 15). Hyaline membrane present, but very thin and difficult to observe, laterally and posteriorly indented. Petiole large, widened in the middle, posterior margin convex. Petiole 184 long (measured from ventral view) and 155 wide. Ligulate process absent. Lengths of PI–V: 41, 91, 89, 118, 73. PIV with a hump; PII with one seta near anteroventral corner and two setae located near the middle of anterior margin (Figure 18). Lengths of I-leg-4-6: 214, 180, 221; lengths of IV-leg-4-6: 291, 194, 184. IV-leg-4 with a long spur.

Female

Body 1140 long and 951 wide. Anterior margin

of body concave. Posterolateral corners very distinct. Gonopore 145 long; genital valves with large chitinous patches, the anterior patch triangular, the posterior patch rounded. Genital plates long, straight and narrow, not extending to lateral body margin, laterally widened (Figure 19). V2 on humps. Lengths of PI–PV: 29, 77, 62, 96, 60. PII with 2 anteroventral and 1 more dorsally located seta on medial side of PII; hump of PIV absent. Lengths of I-leg-4-6: 170, 155, 165; lengths of IV-leg-4-6 223, 175, 165.

Remarks

The male is close to *A. shoesmithi* Wiles from Malaysia (Wiles 1993). This last species has a petiole gradually tapering posteriorly, a trapezoid hyaline membrane with a posterior margin which is only slightly concave, and a dorsal shield not narrowed in the middle. Females of the two species differ in the shape of the genital plates. The male of *A. latipetiolatus* Piersig from the Bismarck-Archipel (Piersig 1903) also has a wide petiole, but this petiole is narrowed anteriorly. For similar species of the female see discussion at *A. harveyi* sp. nov.

Etymology

The species name is derived from the fact that the type locality the Chinderwariner Pool, has an abundant growth of water lilies.

Arrenurus (Arrenurus) mantonensis sp. nov.

Figures 20–24

Material Examined

Holotype

♂, Manton Dam, Northern Territory, Australia, 1 August 1994 (NTM).

Paratypes

Australia: Northern Territory: 1 ♂ (not fully sclerotized) (ZMA), 2 ♀ (one not fully sclerotized) (ZMA, NTM), 2 nymphs (ZMA), same data as holotype.

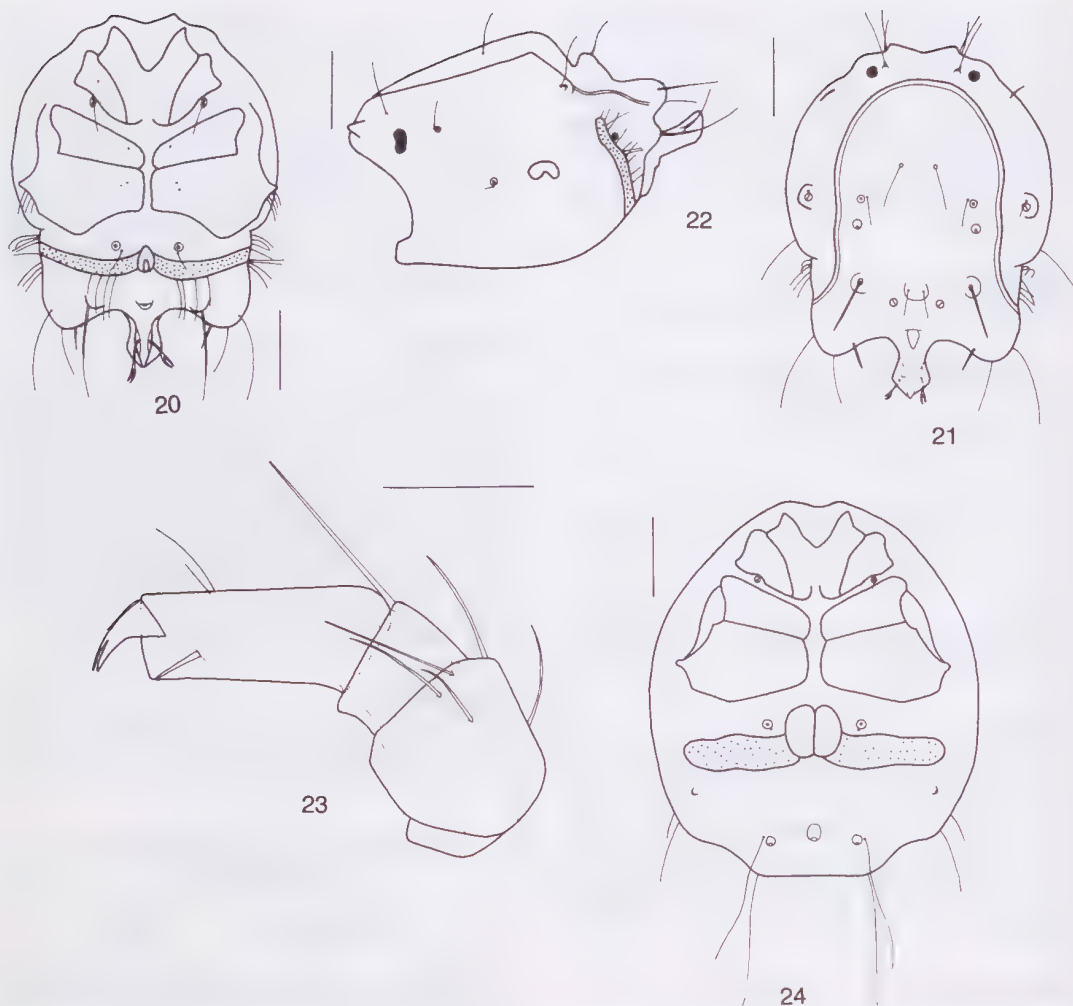
Diagnosis

The very slender PIV is diagnostic for the new species. Petiole with bifurcated setae; hyaline membrane absent.

Description

Male

Body 917 long (including petiole) and 689 wide. Body colour yellowish. Anterior body margin V-shaped. Cauda well developed, pygal lobes short and broad. Dorsal furrow extending onto cauda (Figure 21). D1 on humps, lateral of D4 a seta on

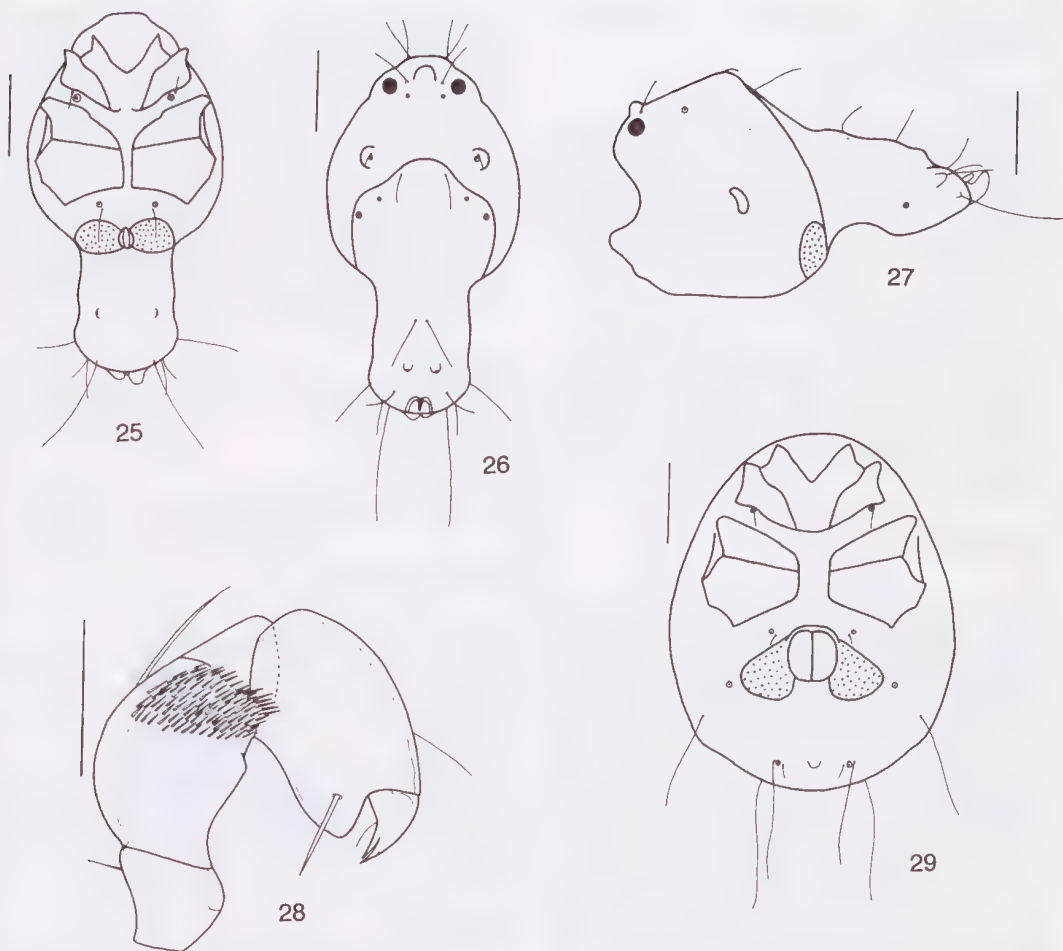


Figures 20–24 *Arrenurus (Arrenurus) mantonensis* sp. nov., holotype ♂ (unless stated otherwise): 20, ventral view; 21, dorsal view; 22, lateral view; 23, palp; 24, ventral view, paratype ♀. Scale lines, 50 μ m (Figure 23), 200 μ m (Figures 20–22, 24).

humps (Figure 22). Gonopore 68 long. Genital plates long and narrow, extending onto lateral side of body (Figure 20). Posterior margin of genital plates with numerous long setae. Petiole 155 long (measured from ventral view) and 102 wide, with a rhomboid hyaline area. Petiole ventrally with two bifurcated setae, medial part of petiole with a finely serrated lateral margin. Hyaline membrane absent. Cauda dorsally with a tubercle, just anterior of petiole. Lengths of PI–PV: 29, 54, 31, 82, 29; PII with 3 setae on medial side, PIV very slender, with a very short anterior margin (Figure 23). Lengths of I-leg-4-6: 146, 136, 194. Lengths of IV-leg-4-6: 204, 165, 112; IV-leg-4 without a spur.

Female

Body 941 long and 844 wide. Anterior body margin slightly concave. Posterolateral corners of body distinct, posterior body part truncated, posterior body margin straight. Dorsal furrow complete, dorsal shield 815 long. D1 on very small humps. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 less than width of one genital valve. Gonopore 107 long, genital valves without chitinous patches. Genital plates long and straight, anterior margin slightly undulating (Figure 24). Lengths of PI–PV: 25, 52, 34, 78, 25; palp as in male. Lengths of I-leg-4-6: 160, 165, 175. Lengths of IV-leg-4-6: 228, 194, 175.



Figures 25–29 *Arrenurus (Megaluracarus) caeruleus* sp. nov., holotype ♂ (unless stated otherwise): 25, ventral view; 26, dorsal view; 27, lateral view; 28, palp; 29, ventral view, paratype ♀. Scale lines, 50 µm (Figure 28), 200 µm (Figures 25–27, 29).

Remarks

The very slender PIV, with the very short anterior margin, is unusual in *Arrenurus*, and easily separates the new species from other members of the genus.

Etymology

Named after the type locality.

Arrenurus (Arrenurus) rouxi Walter

Arrenurus pseudoaffinis (in part, ♀) Piersig, 1906: 360.

Arrenurus rouxi Walter, 1915: 120; Walter, 1928: 259.

Arrenurus rouxi Walter: K. Viets, 1935: 9; Cook, 1967: 228; Lundblad, 1969: 417; Wiles, 1990: 281.

Material Examined

Australia: Western Australia: 1 ♂, Deep Reach Pool, Millstream-Chichester National Park, 15 August 1994 (ZMA).

Remarks

A widespread species, known from New Caledonia, Sumatra, Java, Burma, India, Burma, Singapore, Sri Lanka and Sulawesi. The new record is the first for Australia.

Arrenurus (Megaluracarus) caeruleus sp. nov.

Figures 25–29

Material Examined

Holotype

♂, Pools upstream of Waterfall Creek, Kakadu

National Park, Northern Territory, Australia, 25 July 1994 (NTM).

Paratypes

Australia: Northern Territory: 2 ♂, 6 ♀, same data as holotype (NTM); 2 ♂, Lily Ponds Falls, Katherine Gorge National Park, 27 July 1994 (ZMA); 1 ♂ (WAM), 4 ♀ (WAM, ZMA), Plunge Pool, Edith Falls, Katherine Gorge National Park, 30 July 1994.

Diagnosis

PII with patch of setae; body dorsally with short projection (rostrum). Cauda of male rounded and slightly enlarged posteriorly; posterior margin of cauda with a small, irregular shaped hyaline area. Female with short and broad genital plates, sloping posteriorly.

Description

Male

Body 902 (854–1028) long and 475 (466–524) wide. Body colour blue. Anterior body margin straight. Anterior end of body dorsally with a short projection (rostrum). Dorsal shield incomplete, dorsal furrow extending onto lateral sides of body. D1 on small humps (Figure 27). Cauda well developed, 330 long, posterior part slightly enlarged, posterior margin rounded (Figure 26). Posterior margin of cauda with a small, irregular shaped hyaline area. Gonopore 58 long. Genital plates short, anterior and posterior margins rounded, extending to lateral body margin (Figure 25). Petiole present, dagger-like; one of the paratypes has a double petiole. Lengths of PI–PV: 29, 62, 35, 69, 26; PII with a patch of setae (Figure 28). Lengths of I-leg-4-6: 114, 126, 116. Lengths of IV-leg-4-6: 155, 136, 165; IV-leg-4 with a short, truncated spur.

Female

Body 863 (728–883) long and 698 (611–737) wide. Body slender to broad egg-shaped, posterolateral corners absent or present. Anterior body margin rounded, rostrum short. D1 not on humps. Dorsal shield complete, 427–504 long. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 about as large as width of one genital valve. Gonopore 126 long; genital valves without chitinous patches. Genital plates short and broad, sloping posteriorly (Figure 29). Lengths of PI–PV: 29, 73, 36, 52, 34; palp as in male. Lengths of I-leg-4-6: 116, 126, 97. Lengths of IV-leg-4-6: 165, 175, 165.

Remarks

A small number of species of the subgenus

Megaluracarus have been described from Australia. Most closely related are *A. margatellus* Cook, which differs from the new species in medial projection at the posterior margin of the cauda, and *A. cheetus* Cook, which has a different petiole. The female is very close to *A. thienemanni* K.O. Viets. The dorsal shield of *caeruleus* is smaller, the ratio of body length/length of dorsal shield is 1.58–1.70 for *caeruleus* and 1.39–1.48 for *thienemanni*. Further, *A. caeruleus* does not have the large anterior seta on the dorsal margin of PIV. Like *thienemanni*, females of *caeruleus* are variable in body shape.

Etymology

The species is named for its conspicuous blue colour.

Arrenurus (Megaluracarus) gilvus sp. nov.
Figures 30–34

Material Examined

Holotype

♂, Lily Ponds Falls, Katherine Gorge National Park, Northern Territory, Australia, 27 July 1994 (NTM).

Paratypes

Australia: Northern Territory: 1 ♀, same data as holotype (NTM); 1 ♂, Southern Rockhole, Katherine Gorge National Park, 27 July 1994 (ZMA).

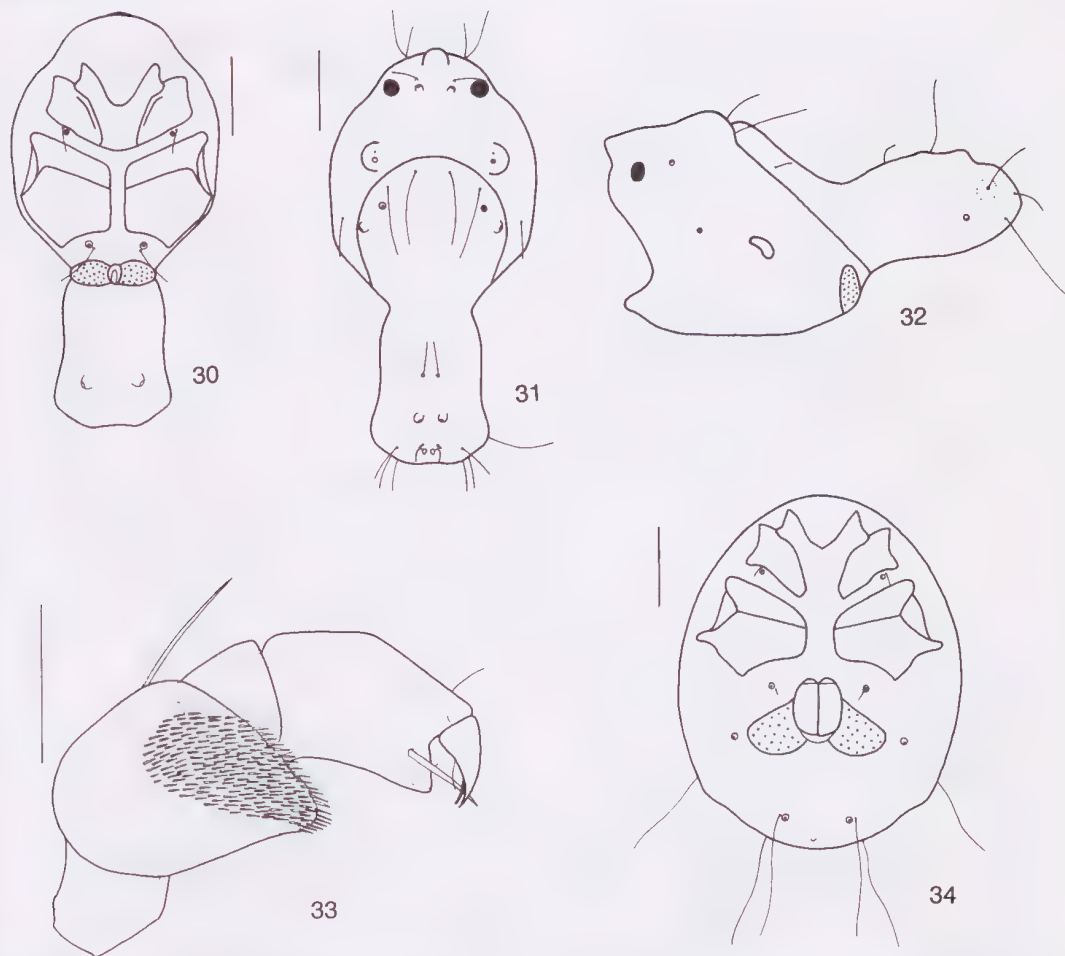
Diagnosis

Body colour yellowish, body dorsally with small rostrum. PII with large patch of setae. Cauda of male posteriorly widened, with straight to slightly concave posterior margin; posterodorsally on cauda two peg-like setae; posterior margin of cauda with small hyaline area. Female with short, broad, posteriorly sloping genital plates.

Description

Male

Body 1048 (1004) long and 524 (495) wide. Body colour yellowish. Anterior body margin rounded, near anterior margin a small rostrum. D1 on small humps (Figure 32). Postocularia and associated setae of D2 very long. Cauda well developed, longer than wide, posteriorly widened, posterior margin of cauda straight to slightly concave (Figure 31). Dorsally on cauda, near posterior margin two rounded peg-like setae; posterior margin of cauda with a very small hyaline area. Genital plates short and broad, extending to lateral body margin (Figure 30). Lengths of PI–PV: 29, 65, 35, 68, 23; PII with large patch of setae on a bulge (Figure 33).



Figures 30–34 *Arrenurus (Megaluracarus) gilvus* sp. nov., holotype ♂ (unless stated otherwise): 30, ventral view; 31, dorsal view; 32, lateral view; 33, palp; 34, ventral view, paratype ♀. Scale lines, 50 μ m (Figure 33), 200 μ m (Figures 30–32, 34).

Lengths of I-leg-4-6: 126, 136, 141. Lengths of IV-leg-4-6: 189, 131, 165; IV-leg-4 with a short, truncated spur.

Female

Body 878 long and 708 wide. Body colour brownish yellow. Anterior body margin rounded. Posterolateral corners of body indistinct. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 larger than width of one genital valve. Genital valves without chitinous patches. Genital plates short and rounded, sloping posteriorly (Figure 34). Lengths of PI–PV: 31, 67, 41, 67, 29; palp as in male. Lengths of I-leg-4-6: 116, 145, 136. Lengths of IV-leg-4-6: 160, 165, 170.

Remarks

A number of females have genital plates similar

to those of *A. gilvus*, e.g. *A. vanderpalae*, *A. caeruleus* sp. nov. and *A. thienemanni*. The last two species differ in having a blue body colour, while the female of *A. vanderpalae* is larger and has more angular genital plates.

Etymology

Named for the light-yellow colour of the male.

Arrenurus (Megaluracarus) thienemanni K.O. Viets

Figures 41–44; 74

Arrenurus thienemanni K.O. Viets, 1984: 432.

Material Examined

Holotype

♂, Roper Valley, Station spring, Northern

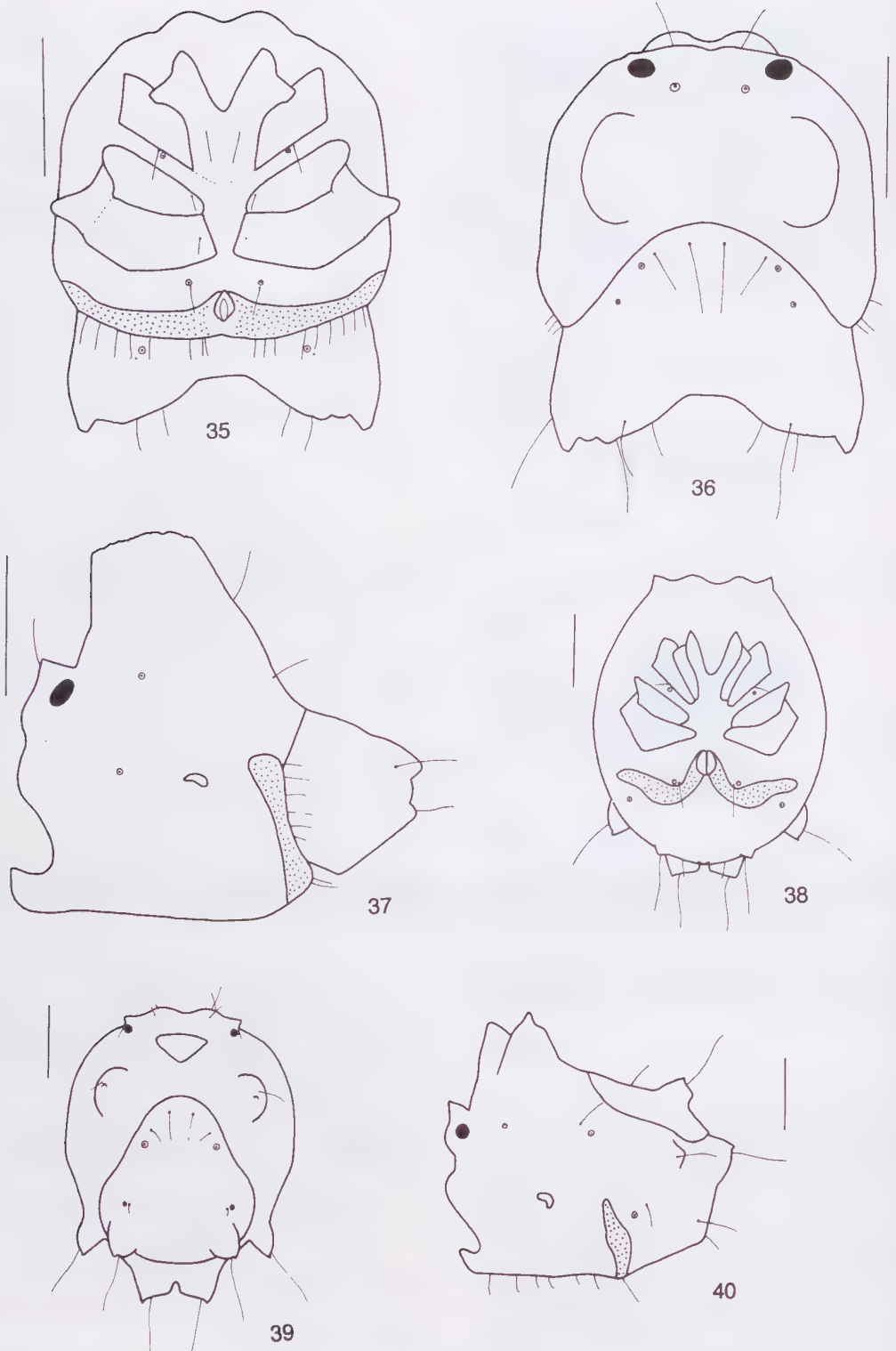
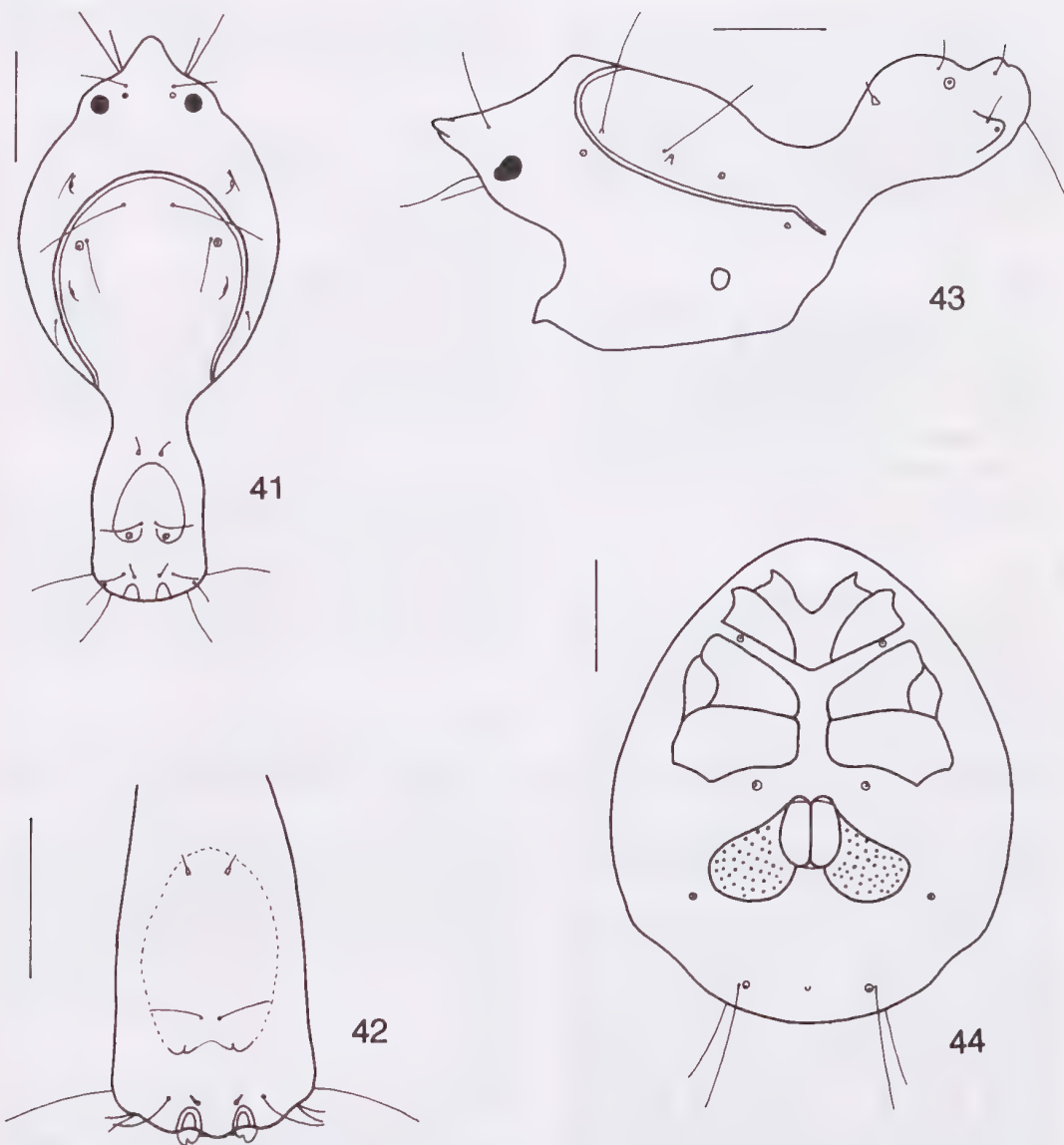


Figure 35–40 *Arrenurus (Breviceaudaturus) lohmanni* Piersig: 35–37, ♂: 35, ventral view; 36, dorsal view; 37, lateral view; 38–40, ♀: 38, ventral view; 39, dorsal view; 40, lateral view. Scale lines, 500 μ m.



Figures 41–44 *Arrenurus (Megaluracarus) thienemanni* K.O. Viets: 41–43, ♂: 41, ventral view; 42, dorsal view cauda; 43, lateral view; 44, ventral view, ♀. Scale lines, 200 μ m.

Territory, Australia, 12 July 1981, B.V. Timms (SMF, slide 7443).

Paratypes

Australia: Northern Territory: 3 ♀, same data as holotype (SMF, slides 7448, 7449, 7450).

Other Material

Australia: Northern Territory: 2 ♂, 3 ♀, Lake Jabiru, Jabiru, 20 July 1994; 2 ♂, 4 ♀, Southern Rockhole, Katherine Gorge National Park, 27 July 1994; 16 ♂, 13 ♀, Pools upstream of Waterfall

Creek, Kakadu National Park, 25 July 1994; 1 ♀, Pool near Jim Jim Falls, Kakadu National Park, 23 July 1994; 4 ♂, Lily Ponds Falls, Katherine Gorge National Park, 27 July 1994 (all ZMA).

Description

Male

The cauda of the male has two indentations in lateral view, one large and one small, with a large, obtuse hump. Viets illustrated the cauda without these indentations, although they can be observed

in the holotype. Body 926–1193 long and 369–524 width. Genital plates short and broad, extending almost to lateral body margin. Posterior margin of cauda in specimens from Waterfall Creek and Lake Jabiru have a hyaline area (see Figure 42), which is also present in the holotype. The cauda of males from Waterfall Creek and Lake Jabiru is in lateral view less upturned than in specimens from other localities.

Female

Body 878 (708–844) long and 737 (533–655) wide. The genital plate is large, short and rounded, sloping posterolaterally. The body shape is broad egg-shaped to slender egg-shaped. Body with indistinct to very distinct posterolateral corners. Dorsal shield 470–592. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 less than width of one genital valve. Gonopore 116 long. Palp as in male.

Remarks

K.O. Viets (1984) described this species from Northern Territory, but examination of the holotype revealed that his description is inaccurate in some aspects for the male. The females found in this study are quite different from the one described by Viets. Examination of the paratype females showed, that the female illustrated by Viets (slide 7448) has slightly larger genital plates, while the female of slide 7449 has much larger genital plates, and is similar to the females of this study.

Below I will give some additional characters for the male and for the female.

A. thienemanni is a highly variable species. The variation in size is large, in males as well as in females. Further, the shape of the cauda of the males and the body shape of the females is variable. As all specimens of this study have the large anterior seta on the dorsal margin of PIV, an unusual character in the genus *Arrenurus*, I assigned all to *A. thienemanni*. The related *A. rostratus* is known to be highly variable as well, especially in the shape of the cauda (Walter 1929).

Arrenurus (Megaluracarus) rostratus degeneratus K.O. Viets

Arrenurus rostratus degeneratus K.O. Viets, 1984: 434.

Material Examined

Australia: Northern Territory: 5 ♂, Lake Jabiru, Jabiru, 20 July 1994 (ZMA).

Remarks

This subspecies is only known from the Northern Territory. The body length of the males from this study varies between 1004 and 1038, the body

width varies between 417 and 427. The holotype a is larger, the body length is 1214 and the body width 482 (K.O. Viets 1984).

Arrenurus (Megaluracarus) vanderpalae Smit Figures 45–46

Arrenurus vanderpalae Smit, 1992: 109.

Material Examined

Australia: Western Australia: 2 ♂, 1 ♀, Kalamina Gorge, pond near falls, Hamersley Range National Park, 13 August 1994 (ZMA); 15 ♂, 8 ♀, Jones River, E. of Roeburne, 17 August 1994 (WAM, ZMA); 5 ♀, Pond Snake Creek, Millstream-Chichester National Park, 17 August 1994 (ZMA).

Male

Body 1135–1320 long, body 466–650 wide. The cauda shows some variation, specimens with a more triangular shaped cauda can be found. The posterior part of the cauda has in fully sclerotized specimens a medial extension, bordered on each side by a hyaline area (Figure 45), which can be seen from a lateral view. IV-leg-4 with a short spur.

Female

Body 1125 (1104–1224) long and 931 (892–931) wide. Body broad egg-shaped, with indistinct posterolateral corners. Medial distance of CX4 about equal length of width of one genital valve. Posterior margin of CX4 directed transversally. Gonopore 155 long. Genital plates short, anterior margin straight and beginning halfway gonopore, posterior margin rounded (Figure 46). Palp as in male, with a patch of setae on PII lying on a bulge. Lengths of PI–PV: 26, 65, 50, 82, 41. Lengths of I-leg-4-6: 150, 146, 126. Lengths of IV-leg-4-6: 213, 213, 179.

Remarks

In addition to the description by Smit (1992), which was based on one male only, some remarks will be made on the male. The female was hitherto unknown and is described above.

Also see the discussion under *A. gilvus* sp. nov.

Arrenurus (Micruracarus) anbangbang sp. nov. Figures 47–50

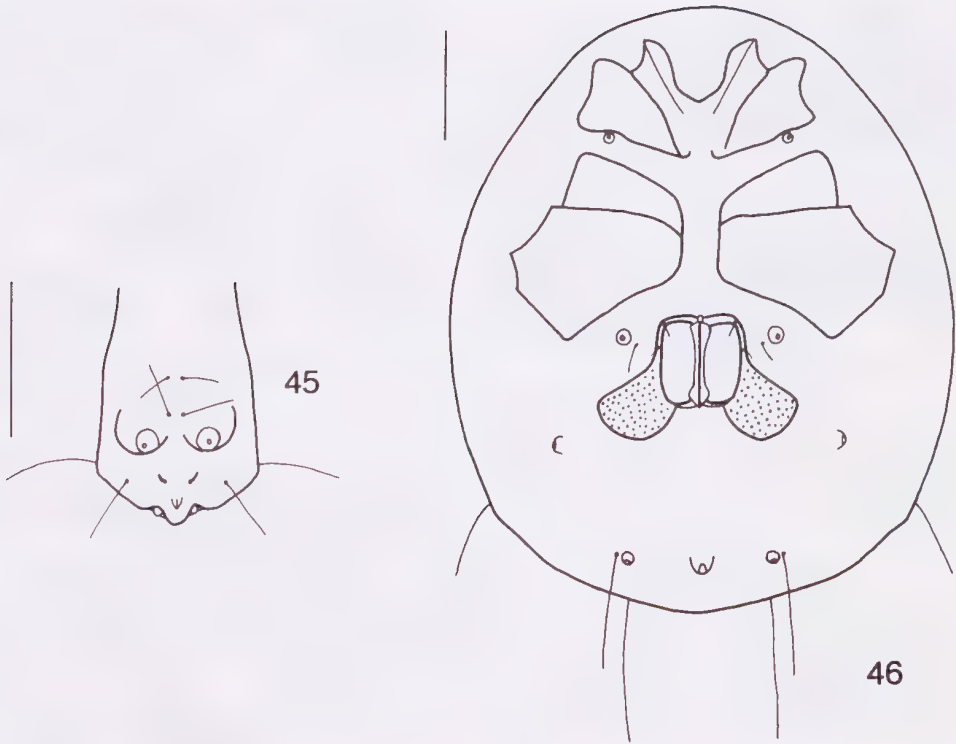
Material Examined

Holotype

♂, Anbangbang Billabong, Kakadu National Park, Northern Territory, Australia, 20 July 1994 (NTM).

Paratypes

Australia: Northern Territory: 2 ♂, 5 ♀, 1



Figures 45–46 *Arrenurus* (*Megaluracarus*) *vanderpalae* Smit: 45, dorsal view cauda, ♂; 46, ventral view, ♀. Scale lines, 200 μ m.

nymph, same data as holotype (NTM); 1 ♂, Billabong Yellow Waters, Kakadu National Park, 21 July 1994 (ZMA); 1 ♂, 1 ♀, Jim Jim Billabong at crossing with Kakadu Highway, Kakadu National Park, 22 July 1994 (ZMA).

Other Material

Australia: Western Australia: 1 ♂, Pond Hancock Gorge, Hamersley Range National Park, 14 August 1994 (WAM); 1 ♂, 9 ♀, Pond Snake Creek, Millstream-Chichester National Park, 17 August 1994 (WAM); 1 ♂, 1 ♀, Jones River, east of Roeburne, 17 August 1994 (ZMA).

Diagnosis

Posterior body margin of male with a cleft, which widens anteriorly; petiole hyaline, tong-shaped; genital plates very narrow, extending onto dorsum. Female with large chitinous patches on genital valves, the anterior patches smaller than the posterior, anterior margin of posterior patch straight; genital plates long, sloping posteriorly and widened laterally.

Description

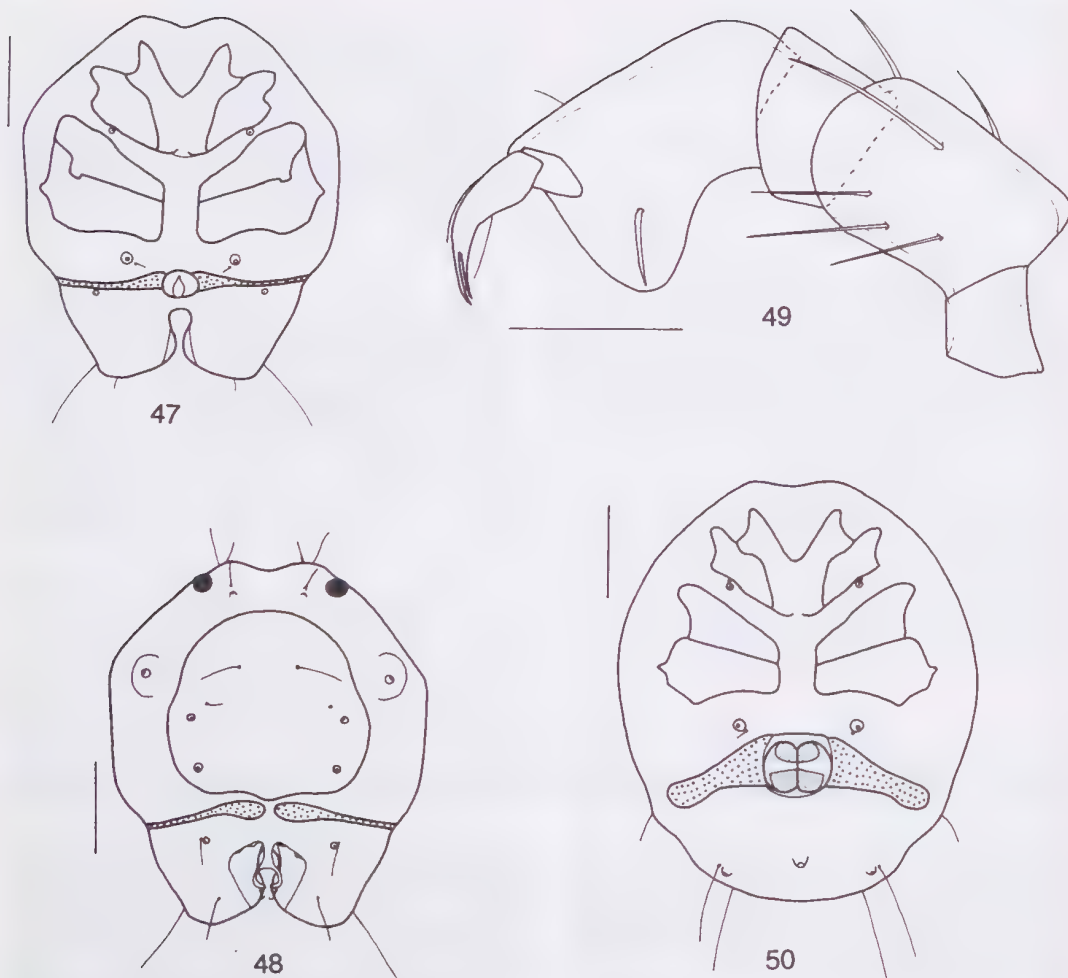
Male

Body 802 (703–786) long and 718 (592–674) wide.

Body colour blue. Anterior body margin concave. Cauda present, caudal lobes rounded. Posterior body margin with a cleft, which widens anteriorly. Dorsal furrow complete; dorsal shield 422 (359–388) long, posterior margin undulating. D1 on humps. Gonopore 48 long. Genital plates long and narrow, extending onto dorsum (Figure 47). Petiole present, hyaline, tong-shaped (Figure 48). Lengths of PI–PV: 29, 53, 38, 84, 43. PII rectangular, with four setae on medial side, PIV with a large, rounded anteroventral corner (Figure 49). Lengths of I-leg-4-6: 112, 116, 136. Lengths of IV-leg-4-6: 170, 146, 116; IV-leg-4 without spur.

Female

Body 912 (776–941) long and 795 (669–805) wide. Anterior body margin slightly concave. Posterolateral corners of body indistinct. Posterior body margin concave, straight or slightly convex. Dorsal furrow complete, dorsal shield 718 (572–708) long. D1 on small humps. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 as large as or smaller than width of genital valve. Gonopore 87 long. Genital valves with large chitinous patches, the anterior smaller than the posterior. Anterior margin of posterior patches straight. Genital plates long, sloping



Figures 47–50 *Arrenurus* (*Micruracarus*) *anbangbang* sp. nov., holotype ♂ (unless stated otherwise): 47, ventral view; 48, dorsal view; 49, palp; 50, ventral view, paratype ♀. Scale lines, 50 μ m (Figure 49), 200 μ m (Figures 47–48, 50).

posteriorly and laterally widened (Figure 50). However, there is much variation in the shape of the genital plates, many females have more bowed genital plates, which are narrowed laterally. Lengths of PI–PV: 29, 58, 41, 84, 41; PII with three setae on medial side, palp as in male. Lengths of I-leg-4-6: 136, 116, 121. Lengths of IV-leg-4-6: 175, 145, 131.

Remarks

The new species is close to *A. forpicatoides* Lundblad. The male of the new species has a free lying petiole, while the petiole of *A. forpicatoides* is fused with the cauda by a hyaline area. According to Lundblad (1947) *A. forpicatoides* has no petiole, but instead a hyaline area, which he supposed to

be homologous with a petiole. However, in my opinion a distinct petiole is present in *forpicatoides*, which is, as stated above, fused with the cauda. Another character that separates the male of the new species from *forpicatoides* is the shape of the caudal lobes (rounded in *anbangbang*, truncated in *forpicatoides*). The female of the new species is close to *A. jabiruensis* sp. nov., *A. madaraszi* Daday and *A. forpicatoides* Lundblad. *A. anbangbang* differs from these three species in the large, pronounced anteroventral corner of PIV. *A. jabiruensis* has less bowed genital plates, but due to the variation in the shape of the genital plates, the differences are small. Further, females of *jabiruensis* have a distinct truncated posterior body part. Females of *A. madaraszi* are very close to the new species, but

differ in broader genital plates and the absence of posterolateral corners of the body. *A. forpicatoides* has shorter genital plates.

Etymology

Named after the type locality.

Arrenurus (Micruracarus) jabiruensis sp. nov.

Figures 51–55

Material Examined

Holotype

♂, Lake Jabiru, Jabiru, Northern Territory, Australia, 20 July 1994 (NTM).

Paratypes

Australia: Northern Territory: 1 ♂, 5 ♀, Lake Jabiru, Jabiru, 20 July 1994 (ZMA); 2 ♀, Pond in

Jim Jim Creek, at Jim Jim Crossing, Kakadu National Park, 22 July 1994 (NTM); 1 ♀, 1 nymph, Small Billabong, Yellow Waters, Kakadu National Park, 22 July 1994 (NTM); 1 ♀, Jim Jim Billabong at crossing with Kakadu Highway, Kakadu National Park, 22 July 1994 (NTM); 1 ♀, Manton Dam, 1 August 1994 (WAM).

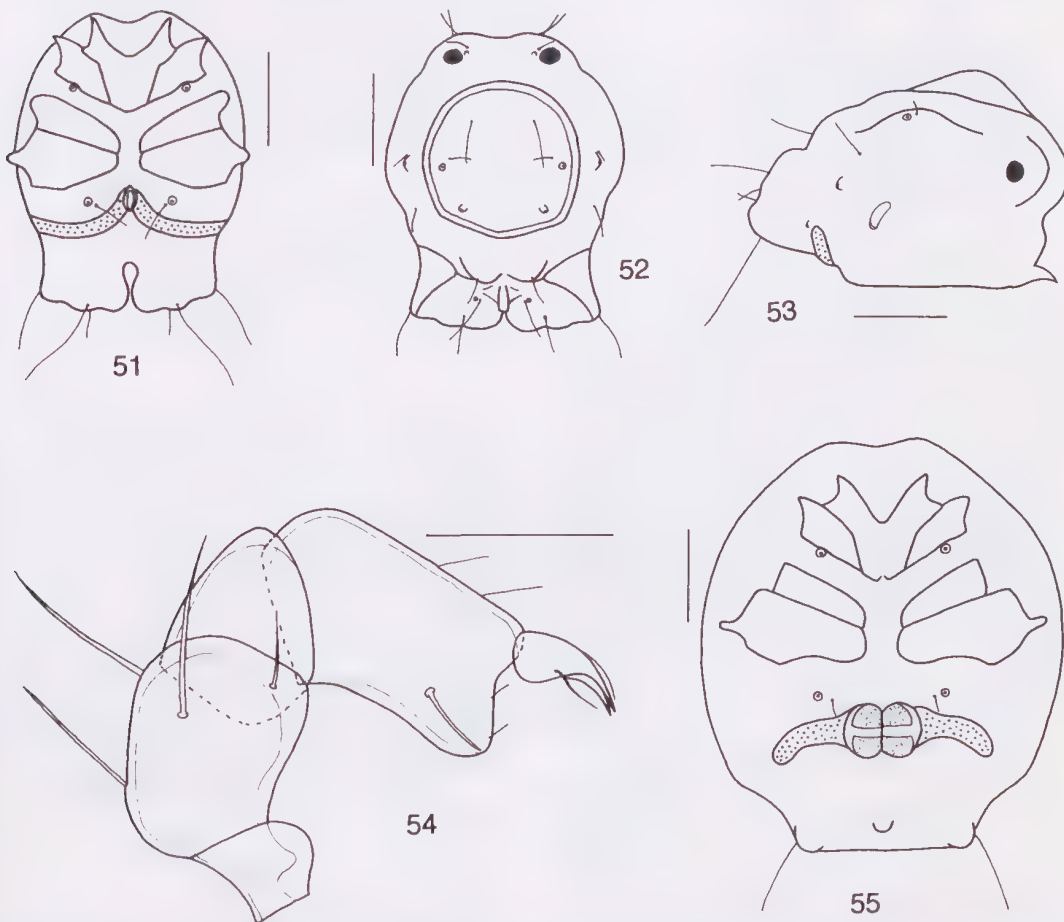
Diagnosis

Cauda of male with a cleft, petiole chisel-shaped; posterior margin of cauda slightly indented. Female with a truncated posterior body part, posterior body margin straight.

Description

Male

Body 650 (698) long and 524 (550) wide. Body colour blue-green. Dorsal furrow complete, dorsal



Figures 51–55 *Arrenurus (Micruracarus) jabiruensis* sp. nov., holotype ♂ (unless stated otherwise): 51, ventral view; 52, dorsal view; 53, lateral view; 54, palp; 55, ventral view, paratype ♀. Scale lines, 50 µm (Figure 54), 200 µm (Figures 51–53, 55).

shield 340 long, without humps, rounded with posterior margin slightly angular. Anterior body margin concave. Cauda well set off from body, with a median cleft. Petiole chisel-shaped, with convex lateral margins and a straight posterior margin (Figure 52). Posterior margin of cauda slightly indented. L3 on obtuse humps; D4 on small humps (Figure 53). Genital plates bowed, narrow, extending onto lateral sides of body (Figure 51). Gonopore 58 long. Lengths of PI-V: 24, 48, 65, 72, 34; PII with two setae on medial side (one large and one small seta) (Figure 54). Lengths of I-leg-4-5: 103, 106, 122; lengths of IV-leg-4-6: 146, 113, 127. IV-leg-4 with a long, pointed spur.

Female

Body 892 (844-931) long and 795 (737-844) wide. Body oval-shaped, truncated posteriorly and with

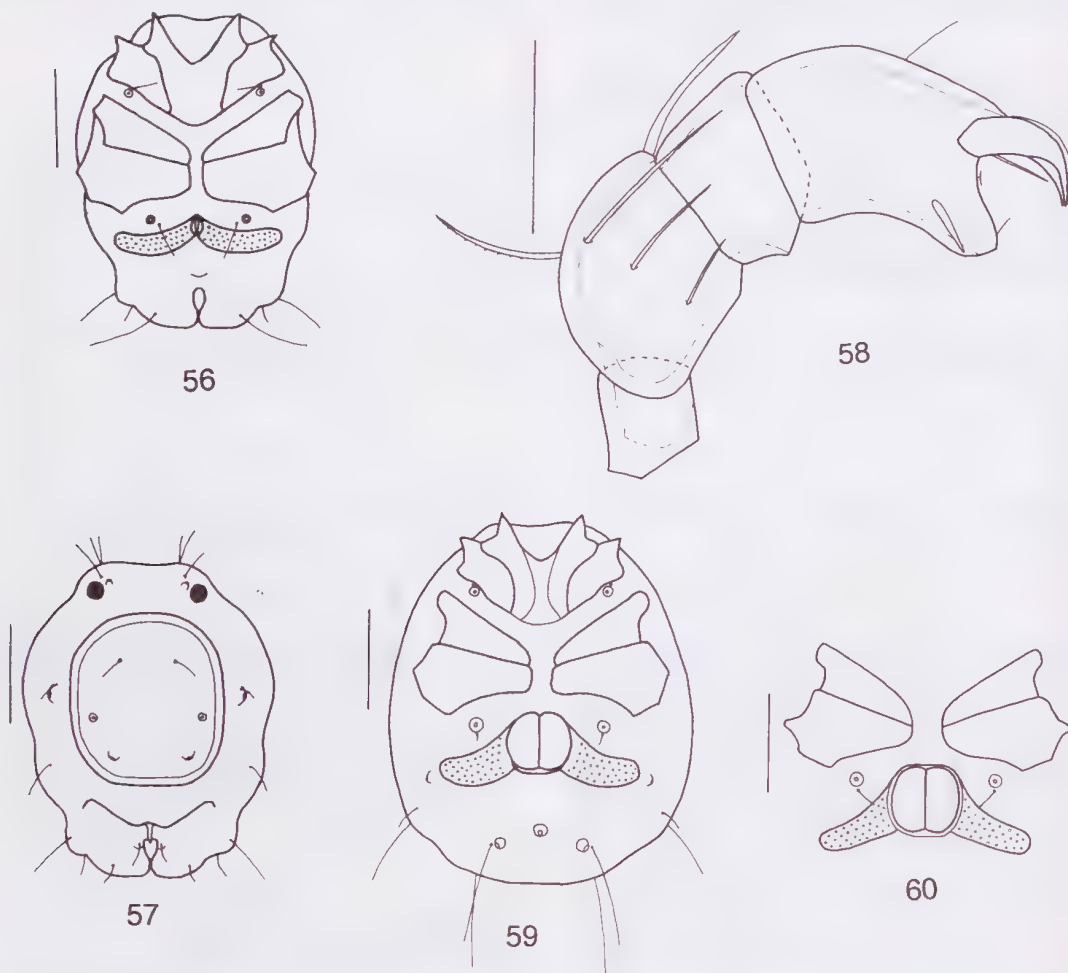
a straight posterior margin (Figure 55). Capitular bay V-shaped. Medial margin of CX4 larger than medial margin of CX3. Distance of CX4 as large as one genital valve. Gonopore 92 long; genital valves with large chitinous patches. Genital plates narrow, geniculated. Lengths of PI-V: 34, 58, 36, 82, 38; PII with 3 setae on medial side. Lengths of I-leg-4-6: 126, 116, 126; lengths of IV-leg-4-6: 155, 145, 136.

Remarks

Females are more difficult to separate from related species, e.g. *A. madaraszii* Daday. The female of the new species has geniculate genital plates, but most characteristic is the truncated posterior body part.

Etymology

The species is named after the type locality.



Figures 56-60 *Arrenurus (Micruracarus) purpureus* sp. nov.: 56-58, holotype ♂: 56, ventral view; 57, dorsal view; 58, palp; a; 59-60, paratype ♀: 59, ventral view; 60, ventral view. Scale lines, 50 µm (Figure 58), 200 µm (Figures 56-57, 59-60).

Arrenurus (Micruracarus) purpureus sp. nov.

Figures 56–60

Material Examined

Holotype

♂, Pond Snake Creek, Millstream-Chichester National Park, Western Australia, Australia, 17 August 1994 (WAM).

Paratypes

Australia: Western Australia: 2 ♂, 13 ♀, same data as holotype (ZMA); 1 ♀, Pond Kalamina Falls, near falls, Hamersley Range National Park, 13 August 1994 (WAM); 2 ♂, 7 ♀, Palm Pool, Millstream-Chichester National Park, 15 August 1994 (WAM); 1 ♀, Chinderwariner Pool, Millstream-Chichester National Park, 15 August 1994 (ZMA); 1 ♂, Crossing Pool, Millstream-Chichester National Park, 16 August 1994 (ZMA); 4 ♀, small pond near Crossing Pool, Millstream-Chichester National Park, 16 August 1994 (NTM); 1 ♀, Python Pool, Millstream-Chichester National Park, 17 August 1994 (ZMA); 2 ♂, Jones River, E. of Roeburne, 17 August 1994 (WAM); 2 ♂, Fortescue River at crossing with Highway, 18 August 1994 (NTM); 1 ♀, Ashburton River, at crossing with North West Coastal Highway, 18 August 1994 (WAM).

Diagnosis

Body colour purple. Male with a closed median cleft and a dagger-like petiole. Females with short and bowed genital plates.

Description

Male

Body 640 (592–660) long and 510 (456–524) wide. Body colour purple. Anterior margin of body slightly concave. Dorsal furrow complete, dorsal shield 359 (310–373) long. D1 on small humps. Cauda short, indistinctly set off from body, with a closed median cleft. Cauda posterolateral indented, forming four lobes (Figure 57). Medial margin of CX4 longer than medial margin of CX3. Just anterior of petiole two fused tubercles. Petiole simple, dagger-like. Gonopore 43 long. Genital plates bowed, not extending to lateral body margin (Figure 56). Lengths of PI–PV: 26, 53, 36, 67, 34; PII with 3 setae on medial side (Figure 58). Lengths of I-leg-4-6: 107, 107, 116. Lengths of IV-leg-4-6: 146, 102, 126; IV-leg-4 with a spur.

Female

Body 737 (689–873) long and 621 (592–723) wide. Anterior body margin slightly concave. Posterolateral corner of body indistinct. Dorsal shield 582 (534–669) long and 480 (412–504) wide. Dorsum without humps. Medial margin of CX4 larger than medial margin of CX3. Medial distance

of CX4 smaller than width of one genital valve. In some specimens the posteromedial corner of CX4 is almost absent (Figure 60). Gonopore 111 long, genital valves without chitinous patches. Genital plates short and narrow, (slightly) bowed (Figure 59). Lengths of PI–PV: 36, 74, 46, 62, 34; PII with 4 setae on medial side. Lengths of I-leg-4-6: 107, 116, 107. Lengths of IV-leg-4-6: 155, 160, 131.

Etymology

The species is named for its purple colour.

Arrenurus (Micruracarus) separatus sp. nov.

Figures 61–64

Material Examined

Holotype

♂, Pond Dales Gorge, Hamersley Range National Park, Western Australia, Australia, 12 August 1994 (WAM).

Diagnosis

Male without cauda, pygal lobes and petiole; body posteriorly with a concavity, with a complicated structure; genital plates separated medially, not fused with gonopore.

Description

Male

Body 587 long and 495 wide. Body colour yellowish brown, legs purple. Anterior body margin convex. Cauda, pygal lobes and petiole absent (Figure 62). Dorsal furrow incomplete, passing onto posterior body part. Body posteriorly with a concavity, in which a complicated structure is visible, which is better illustrated than described (Figure 63). Posterior body margin with a small notch. Gonopore 29 long. Genital plates separated, not fused with gonopore (Figure 61). Lengths of PI–PV: 41, 110, 70, 103, 49; PII with two setae on medial side (Figure 64). Lengths of I-leg-4-6: 111, 126, 97. Lengths of IV-leg-4-6: 160, 131, 136; IV-leg-4 without a spur; third and fourth legs with numerous swimming setae.

Female

Unknown.

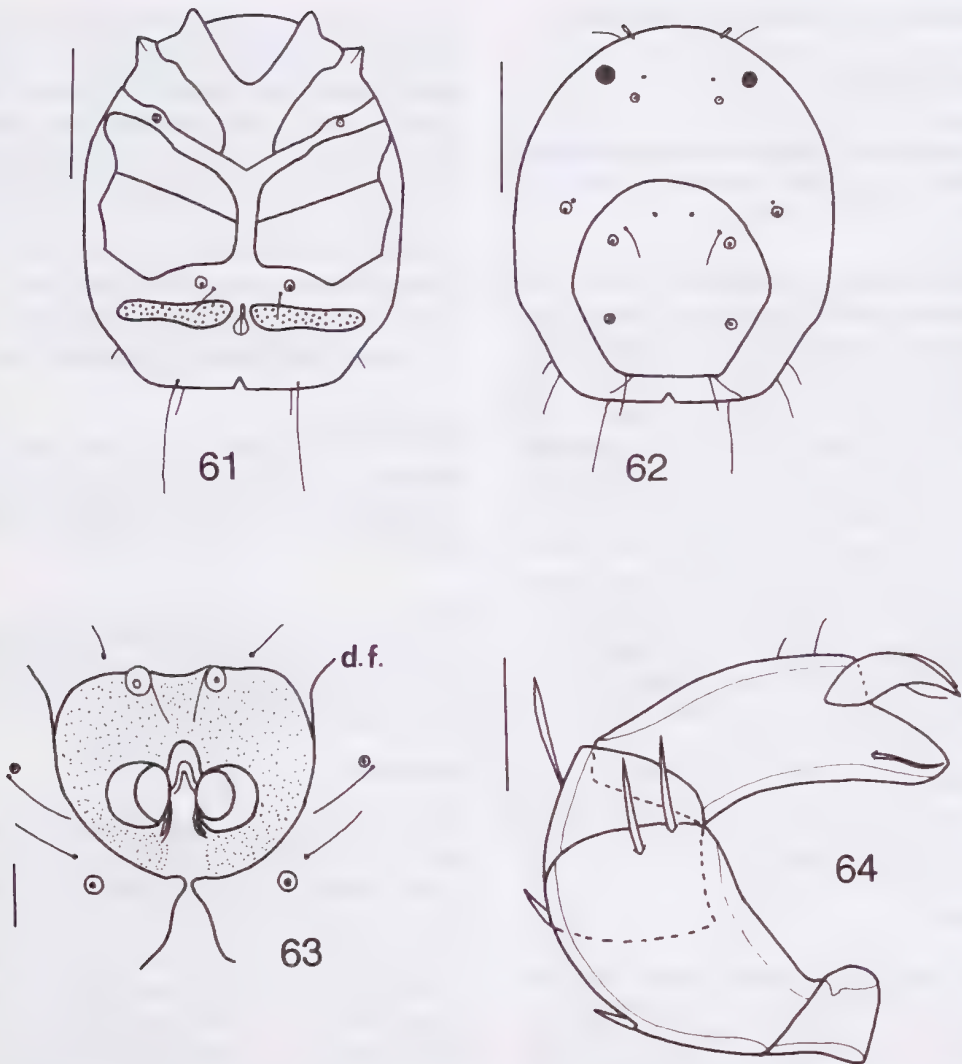
Etymology

Named after its separated genital plates.

Arrenurus (Rhinophoracarus) gracilipes Piersig

Arrhenurus gracilipes Piersig, 1906: 370.

Rhinophoracarus gracilipes Piersig: K. Viets, 1935: 2; Lundblad, 1969: 392.



Figures 61–64 *Arrenurus (Micruracarus) separatus* sp. nov., holotype ♂: 61, ventral view; 62, dorsal view; 63, posterior view; 64, palp. Scale lines, 50 µm (Figures 63–64), 200 µm (Figures 61–62). d.f. = dorsal furrow.

Material Examined

Australia: Northern Territory: 2 ♂, Lake Jabiru, Jabiru, 20 July 1994 (ZMA).

The first record of this subgenus for Australia. *A. gracilipes* is widespread, and reported from India, Sumatra and Java.

Arrenurus (Brevicaudaturus) subgen. nov.

Type species

Arrenurus lohmanni Piersig, 1898.

Diagnosis

Male

Characters of Arrenuridae. Dorsal shield present, dorsal furrow complete or passing onto lateral sides. Cauda short and wide, posteriorly with a median cleft. D1 on very large humps.

Female

D1 on very large humps.

Remarks

The taxonomic position of this very distinct

group of water mites has puzzled acarologists for a long time. K. Viets (1956) placed species of this group in the subgenus *Micruracarus*, probably because the presence of a median cleft in the cauda. Later, Cook (1957) assigned this group to the subgenus *Megaluracarus*. However, species of the new subgenus are very different from all *Megaluracarus* species. All members of the new subspecies have D1 on very large humps, and many species have other large humps on the dorsum or one hump between the humps of D1, which give them a very three-dimensional appearance.

The following species belong to the new subgenus (all **comb. nov.**): *A. lohmanni*, *A. bicornutus* Piersig, *A. laticodulus* Piersig, *A. matupitensis* Piersig, *A. quadricornutus* Piersig, *A. multicornutus* Walter, *A. toxopeusi* K. Viets, *A. tricornutus* K. Viets, *A. roobeeki* Smit (all from the Indo-Australian region and the Pacific), *A. imperator imperator* Lundblad, *A. imperator goliath* Lundblad, *A. guatemaltecus* K.O. Viets, *A. toriger* K. Viets (all from the neotropics), *A. gibbus* Koenike, *A. palpebratus* Nordenskiöld, *A. dumazeri* Molas, *A. neolaticodulus* Cook, *A. discretus* Cook (all from Africa).

***Arrenurus (Brevicaudaturus) lohmanni* Piersig,
comb. nov.
Figures 35–40**

Arrenurus lohmanni Piersig, 1898: 572.

Arrenurus lohmanni Piersig: Piersig, 1903: 21.

Arrenurus lohmanni Piersig: Cook and Bright 1983: 198.

Material Examined

Australia: Western Australia: 1 ♂, 8 ♀, McKenzie Spring, Millstream-Chichester National Park, 17 August 1994 (ZMA).

Description

Male

Body 1464 long, 1176 wide and 1350 high. Two large humps on the anterior body part not fully sclerotized (Figures 36, 37). The corners of the cauda are bluntly-pointed, but are probably not fully sclerotized as well (Figure 35). Lengths of PI–PV: 45, 113, 65, 122, 55; PII with three setae on medial side. Lengths of I-leg-4-6: 194, 213, 310. Lengths of IV-leg-4-6: 320, 291, 252.

Female

Body 2040 (1848–2148) long, 1608 (1464–1680) wide and 1824 (1632–1944) high. Body colour yellow. Anterior part of body with three large, conical humps, D1 on the two lateral humps,

medial hump without glandularia (Figure 39); the humps of D1 narrowed dorsally (Figure 40), the medial hump of equal wide. Dorsal furrow complete, dorsal shield pear-shaped. Dorsal shield 1152 long, with one pair of large humps, on which D4 are situated. Posterior body margin indented. L4 on a small hump. Coxal field small. CX4 almost without medial margin. Gonopore 142 long. Genital plates long and narrow, strongly bowed, extending onto lateral side of body, halfway lateral end of genital plates widened (Figure 38). E4 situated posteriorly of gonopore. Lengths of PI–PV: 55, 136, 79, 140, 60. PII with four setae on medial side, palp as in male. Lengths of I-leg-4-6: 242, 252, 378; Lengths of IV-leg-4-6: 369, 340, 272.

Remarks

A little known but widespread species, reported from the Bismarck Archipelago, Buru and the Palau Islands. This record is the first for Australia. The female has not been previously described.

The male resembles in most aspects the descriptions of Piersig (1903) and Cook and Bright (1983). The specimen of Cook and Bright is smaller (body length 1200) and the genital plate is wider than my own specimen and that of Piersig. The female has three large humps on the anterior body part, while the male has only two. Cook and Bright suspected that *A. matupitensis* Piersig was the female of *A. lohmanni* (a female without humps on the dorsal shield). Now that male and female have been found together, this assumption must be rejected. The female of *A. lohmanni* is close to *A. tricornutus* K. Viets, which has a very similar body shape and configuration of the large humps. *A. tricornutus* is smaller, the small humps near the eyes are more pointed, the anterior body margin is more concave and the genital plate is over its whole length of equal width.

***Arrenurus (Brevicaudaturus) tricornutus* K. Viets**

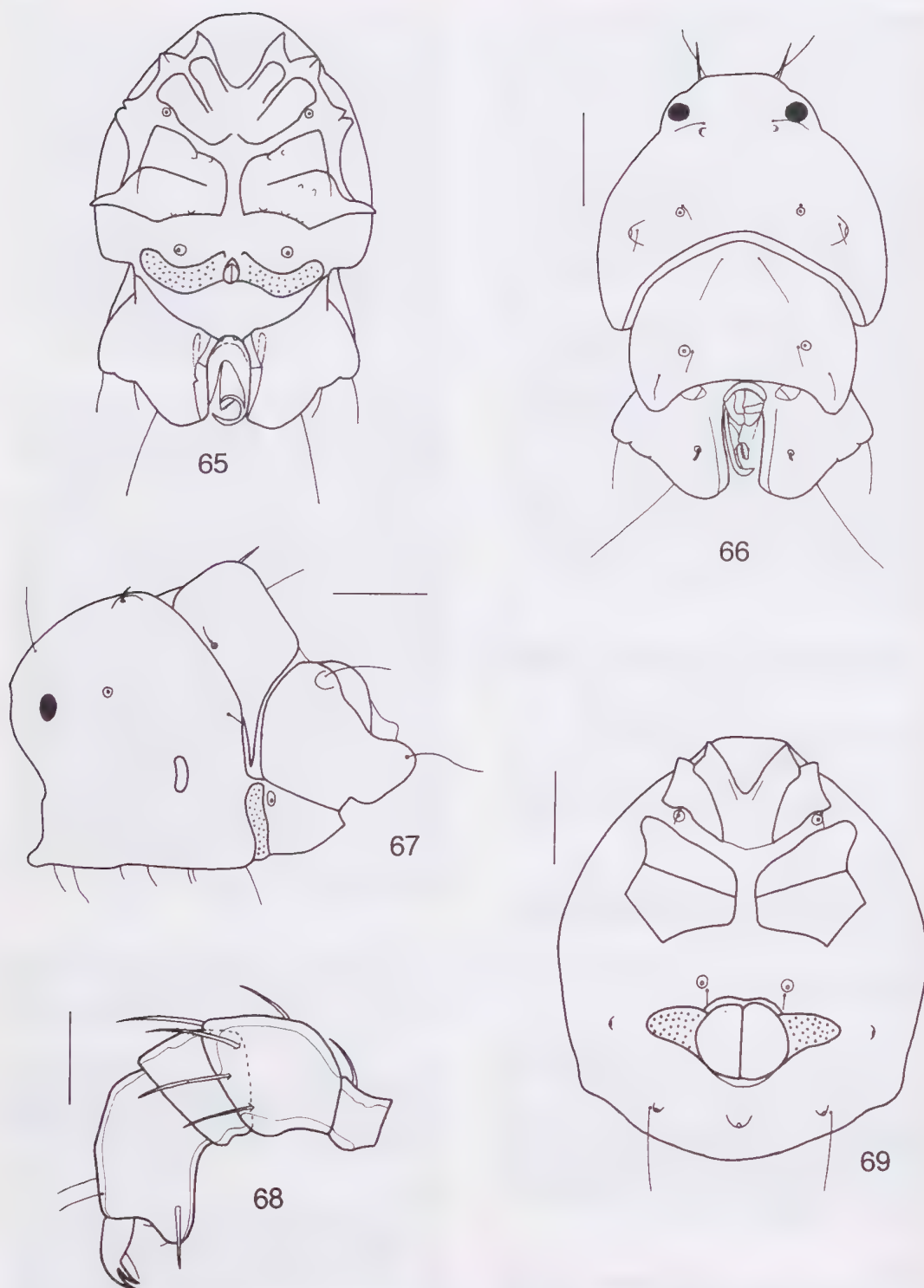
Arrenurus tricornutus K. Viets, 1955: 25; K.O. Viets, 1975: 93; Smit, 1992: 106.

Material Examined

Australia: Northern Territory: 4 ♂, 4 ♀, Small Billabong, Gunlon, Kakadu National Park, 25 July 1994 (ZMA).

Remarks

So far, this species has only been reported from Queensland (K. Viets 1955; Smit 1992). Females from this study vary in body length from 1548–1764 and in body width from 1248–1392, males vary in body length from 1248–1399 and in body width from 1032–1128. The males are thus smaller than specimens from eastern Australia.



Figures 65–69 *Arrenurus (Dividuracarus) tripartitus* sp. nov., holotype ♂ (unless stated otherwise): 65, ventral view; 66, dorsal view; 67, lateral view; 68, palp; 69, ventral view, paratype ♀. Scale lines, 50 μm (Figure 68), 200 μm (Figures 65–67, 69).

Arrenurus (Dividuracarus) subgen. nov.**Type species***Arrenurus (Dividuracarus) tripartitus* sp. nov.**Diagnosis***Male*

Characters of Arrenuridae. Body divided in three parts with complete suture lines, middle part analogous with dorsal shield. Posterior part with a large median cleft. D1 and D2 on anterior body part, close to each other, D3 and D4 on posterior body part. No petiole present, but instead a protrusible, hyaline tube-like structure.

Female

Without subgeneric characters. Genital plates reversed bowed.

Remarks

The very unusual division of the body together with the tube-like structure is not found in any of the Arrenuridae.

Arrenurus (Dividuracarus) tripartitus sp. nov.

Figures 65–69

Arrenurus spec. B Smit, 1992: 110.

Material Examined*Holotype*

♂, Jones River, east of Roeburne, Western Australia, Australia, 17 August 1994 (WAM).

Paratypes

Australia: Queensland: 1 ♀, Cloncurry River, Cloncurry, Queensland, 14 August 1989 (ZMA). **Western Australia:** 1 ♀, Fortescue Falls (pool), Hamersley Range National Park, 11 August 1994 (ZMA); 1 ♀, Pond Kalamina Gorge, near falls, Hamersley Range National Park, 13 August 1994 (WAM); 1 ♂, 2 ♀, 1 nymph, Palm Pool, Millstream-Chichester National Park, 15 August 1994 (ZMA); 1 ♂, 4 ♀, Small pond near Crossing Pool, Millstream-Chichester National Park, 16 August 1994 (WAM); 1 ♂, 2 ♀, Pond Snake Creek, Millstream-Chichester National Park, 17 August 1994 (NTM); 1 ♀, Ashburton River at crossing with North West Coastal Highway, 18 August 1994 (ZMA).

Diagnosis

As for subgenus. Body colour orange to yellow. Ventral body part of male extending well beyond dorsal body part. Female with distinct posterolateral corners of the body.

Description*Male*

Body 922 (912–931) long (without tube-like structure) and 621 (592–640) wide. Body colour orange to yellow. Body divided in three parts, with complete suture lines (Figure 67). Posterior body part with a large median cleft. Suture lines between CX1 and CX2 and between CX3 and CX4 incomplete. Gonopore 48 long. Genital plates bowed, not extending to lateral body margin (Figure 65). No normal petiole present, but a complicated, hyaline tube-like structure with the anterior part rounded and sclerotized; hyaline tube protrusible, open posteriorly and laterally, with serrated lateral margins (Figure 66). D2 shifted to anterior body part, D3 and D4 on middle part, D3 shifted laterally. Lengths of PI–PV: 31, 79, 48, 84, 38; PII with 2 setae on medial side (Figure 68). Lengths of I-leg-4-6: 116, 116, 97; lengths of IV-leg-4-6: 175, 155, 163. IV-leg-4 without a spur; second, third and fourth legs with numerous swimming setae.

Female

The female has been referred to by Smit (1992) as *Arrenurus* spec B. Body 892 (854–946) long and 752 (698–800) wide. Body with distinct posterolateral corners. Dorsal furrow incomplete, dorsum without humps. Medial margin of CX4 larger than medial margin of CX3. Medial distance of CX4 less than width of one genital valve. Gonopore 155 long; genital valves without chitinous patches. Genital plates short, reversed bowed (Figure 69). Posterior body part truncated. Lengths of PI–PV: 34, 86, 58, 82, 46; PII with three setae on medial side. Lengths of I-leg-4-6: 116, 116, 92. Lengths of IV-leg-4-6: 184, 194, 155. Second, third and fourth legs with numerous swimming setae.

Remarks

For discussion see *A. gerecke* sp. nov.

Etymology

The species is named for the division of the body in three parts.

Arrenurus (Dividuracarus) gerecke sp. nov.

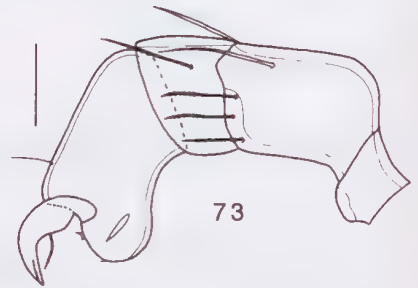
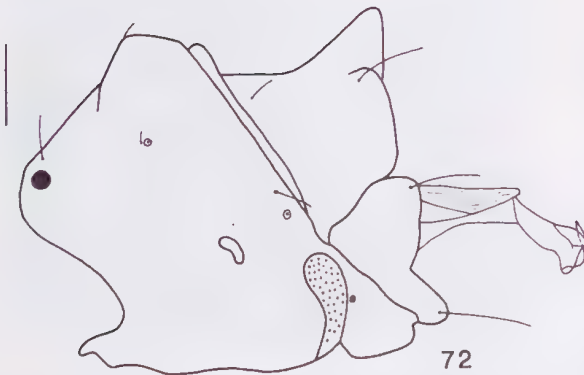
Figures 70–73

Material Examined*Holotype*

♂, Lake Jabiru, Jabiru, Northern Territory, Australia, 20 July 1994 (NTM).

Paratype

Australia: Northern Territory: 1 ♂ (not fully sclerotized), same data as holotype (ZMA).



Figures 70–73 *Arrenurus (Dividuracarus) gereckei* sp. nov., holotype ♂: 70, ventral view; 71, dorsal view; 72, lateral view; 73, palp. Scale lines, 50 μ m (Figure 73), 200 μ m (Figures 70–72).



Figure 74 *Arrenurus (Megaluracarus) thienemanni* K.O. Viets, ♂, outer side PIV and PV. Scale line, 50 μ m.

Diagnosis

As for subgenus. Body colour brownish-green; dorsal posterior body part with a large, conical hump. Ventral posterior body part extending little beyond dorsal posterior body part.

Description

Male

Body 1028 long (without tube-like structure) and 815 wide. Body colour brownish-green. Anterior margin of body slightly concave. Body divided in three parts, with complete suture lines (Figure 72). Ventral posterior body part with a large median cleft, dorsal posterior body part with a large,

conical hump. D1 on a hump, D2 lateral of this hump on posterior dorsal body part. Medial margin of CX3 longer than medial margin of CX4; CX4 without posteromedial corner. Gonopore 58 long. Genital plates long and bowed, extending onto lateral sides of body (Figure 70). Petiole a protrusible hyaline, tube-like structure, open posteriorly, at basis with a scissor-like sclerotization (Figure 71). Lengths of PI–PV: 36, 98, 72, 110, 53. PII with 4 setae on medial side; PIV with a rounded anteroventral corner (Figure 73). Lengths of I-leg-4-6: 165, 150, 136. Lengths of IV-leg-4-6: 281, 170, 184; IV-leg-4 without a spur; second, third and fourth legs with numerous swimming setae.

Female

Unknown.

Remarks

A. gerecke can be separated from the *A. tripartitus* by its body colour, the large, conical hump on the posterior dorsal body part and the shape of the body (ventral posterior body part less extending beyond dorsal posterior body part).

Etymology

The species is named after Dr R. Gerecke.

ACKNOWLEDGEMENTS

I am indebted to Dr M.S. Harvey for his help with the preparations for this trip and for his comments on the manuscript, to the Department of Conservation and Land Management (Perth), the Australian National Parks and Wildlife Service (Darwin) and the Conservation Commission of the Northern Territory (Palmerston) for their permission to collect water mites in the national parks of Western Australia and Northern Territory, to G.M. van der Pal for her assistance with the fieldwork and to Dr M. Grasshoff (SMF) for the loan of type material of *A. thienemanni*.

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- * In Smit (1992) I supposed that the year of publication should be 1948, as the *Arkiv för Zoologi* 40A (2) has been published in that year. However, the separatum is dated 1947, and has apparently been published earlier.

Key to the Australian *Arrenurus*

Key to the subgenera (males only)

1. With a petiole or protrusible, hyaline tube-like structure, usually with pygal lobes; if pygal lobes are absent with a distinct petiole extending well beyond posterior margin of body 2
Without pygal lobes or without petiole extending beyond posterior body end 4
2. No petiole present but instead a protrusible, hyaline tube-like structure (Figure 66), body divided in three parts (Figure 67) *Dividuracarus* subgen. nov.
Petiole present, body not divided in three parts 3
3. Petiole with a large membranous extension, pygal lobes poorly developed (K. Viets 1935, figure 115a) *Rhinophoracarus*
(Only one species known from Australia, i.e. *Arrenurus gracilipes* Piersig)
Petiole without membranous extension, if pygal lobes are reduced, petiole is large and extending well beyond posterior end of body *Arrenurus*
4. Cauda long (more than 1/2 of body length), narrower than body and usually well set off from body *Megaluracarus*
Cauda short 5

5. Cauda not set off from body, without notch, petiole absent *Truncaturus*
Cauda well set off from body 6
6. Cauda short and wide, posteriorly with a median cleft, D1 on very large humps *Brevicaudaturus* subgen. nov.
Cauda often with a notch posteriorly, small petiole often present but not extending beyond posterior body margin, D1 not on large humps *Micruracarus*

Key to the males of *Arrenurus* s.s.

1. Petiole with bifurcated setae (Figure 21) *A. mantonensis* sp. nov.
Petiole without bifurcated setae 2
2. Petiole with ligulate process 3
Petiole without ligulate process 5
3. Ligulate process short, not extending to posterior margin of petiole (Lundblad 1947, figure 45A), body colour reddish-brown *A. australicus* Lundblad
Ligulate process long, extending to posterior margin of petiole, body colour blue to green 4
4. Ligulate process anvil-shaped (Figure 10) *A. harveyi* sp. nov.
Ligulate process spoon-shaped (K. Viets 1935, figure 119a) *A. pseudoaffinis* Piersig
5. Petiole sword-like (Figure 3) *A. ensifer* sp. nov.
Petiole wider, not sword-like 6
6. Pygal lobes very small, not extending beyond posterior body margin (K. Viets 1935, figure 118) *A. rouxi* Walter
Pygal lobes well developed, extending beyond posterior body margin 7
7. Petiole wider than long (in dorsal view) (Figure 16) *A. liliaceus* sp. nov.
Petiole narrower than long 8
8. Petiole truncated, contracted in the middle (Cook 1986, figure 1628) *A. balladoniensis* Halik
Petiole rounded posteriorly, not contracted in the middle, sometimes with a small notch posteriorly (Cook 1986, figure 1632) *A. fissipetiolatus* Lundblad

Key to the males of *Arrenurus* (*Megaluracarus*)

1. Cauda posteriorly with a rudimentary petiole 2
Rudimentary petiole absent 8

2. Cauda as wide as long 3
Cauda distinctly longer than wide 4
3. Cauda posteriorly with a large, hyaline area
(K.O. Viets 1978, figures 33, 34) *A. victorianus* K.O. Viets
Cauda without hyaline area (Cook 1986, figure
1649) *A. cheetus* Cook
4. Cauda with triangular posterolateral
projections (Cook 1986, figure 1651) *A. otodus* Cook
Cauda without triangular posterolateral
projections 5
5. Posterior margin of cauda with a medial
projection (Cook 1986, figure 1639) *A. margatellus* Cook
Posterior margin of cauda without a projection
..... 6
6. Body colour blue, rudimentary petiole dagger-
like (Figure 26) *A. caeruleus* sp. nov.
Body colour yellow or orange 7
7. Two closely situated rudimentary petioles
present, these peg-like (Figure 45) *A. vanderpalae* Smit
Two well separated rudimentary petioles
present, these rounded (Figure 31) *A. gilvus* sp. nov.
8. Dorsal furrow incomplete (Figure 41) *A. thienemanni* K.O. Viets
Dorsal furrow complete 9
9. Cauda short, almost as wide as long (Walter
1929, figure 32) *A. harpagopalpus* Walter
Cauda longer than wide 10
10. Posterior margin of cauda triangular shaped
(K.O. Viets 1984, figure 51) *A. rostratus degeneratus* K.O. Viets
Posterior margin of cauda rounded (Cook
1967, figure 835) *A. rostratus* Daday

**Key to the males of *Arrenurus* (*Brevicaudaturus*)
subgen. nov.**

1. Cauda posteriorly with large hump (Smit 1992,
figure 59) *A. roobeeki* Smit
Cauda without large hump 2
2. Anterior body part with three large humps,
posterior margin of dorsal shield medially
convex (Smit 1992, figure 55) *A. tricornutus* K. Viets
Anterior body part with two large humps,
posterior margin of dorsal shield medially
straight (Figure 36) *A. lohmanni* Piersig

Key to the males of *Arrenurus* (*Micruracarus*)

1. Dorsal shield covering entire dorsum (Smith
and Harvey 1989, figure 1) *A. kitchingi* Smith and Harvey
Dorsal shield smaller than dorsum 2
2. Petiole absent, body posteriorly with a
concavity, genital plates separated, not fused
with gonopore (Figure 61) *A. separatus* sp. nov.
Petiole present 3
3. Petiole tong-shaped 4
Petiole not tong-shaped 5
4. Petiole connected with cauda by a hyaline
area, petiole open posteriorly (Lundblad
1947, figure 48A) *A. forpicatoides* Lundblad
Petiole separated from cauda, petiole almost
closed posteriorly (Figure 48) *A. anbangbang* sp. nov.
5. Petiole chisel-shaped (Figure 52) *A. jabiruensis* sp. nov.
Petiole dagger-like (Figure 57) *A. purpureus* sp. nov.

Key to the males of *Arrenurus* (*Truncaturus*)

1. Posterior body margin with a notch (Cook
1986, figure 1656) *A. haswelli* Cook
Posterior body margin without notch 2
2. Body elongated (Lundblad 1947, figure 49A) ... *A. tasmanicus* Lundblad
Body short (Lundblad 1947, figure 50A) *A. novaehollandiae* Lundblad

**Key to the males of *Arrenurus* (*Dividuracarus*)
subgen. nov.**

1. Body colour orange-yellow, ventral body part
extending well beyond dorsum, D1 on small
humps (Figure 66) *A. tripartitus* sp. nov.
Body colour brownish-green, ventral body
part extending a little beyond dorsum, D1
on large humps (Figure 71) *A. gereckeii* sp. nov.

Key to the females (all subgenera)

1. Genital valves with chitinized patches 2
Genital valves without chitinized patches 13
2. Chitinized patches small, consisting of only a
small strip at anterior and posterior part of
genital valve 3
Chitinized patches large 6

3. Large species ($> 1800 \mu\text{m}$), dorsal shield slender (Figure 2) *A. balladoniensis* Halik
Smaller species ($1000\text{--}1500 \mu\text{m}$) 4
4. Dorsal shield covering entire dorsum, genital field close to coxal field (Cook 1986, figure 1654) *A. haswelli* Cook
Dorsal field distinctly smaller than dorsum ... 5
5. Genital plate fused with genital valve over whole lateral margin of genital valve, larger species ($> 1400 \mu\text{m}$) (Figure 6) *A. ensifer* sp. nov.
Genital plate fused only over a small posterior part of genital valve (Walter 1929, figure 39), smaller species ($1000\text{--}1200 \mu\text{m}$) *A. rouxi* Walter
6. With large posterolateral corners of body 7
Posterolateral corners of body small or absent 9
7. Anterior and posterior chitinized patches of genital valve small, connected by a small strip of pigmentation (Figure 14) *A. harveyi* sp. nov.
Chitinized patches large 8
8. Anterior and posterior patches of genital valve separated (Figure 19) *A. liliaceus* sp. nov.
Anterior and posterior patches of genital valve fused (Walter 1928, figure 42) *A. pseudoaffinis* Piersig
9. Genital plates short (< 2 times as large as wide) (Lundblad 1947, figure 45E) *A. australicus* Lundblad
Genital plates longer ($>$ times as large as wide) 10
10. Genital plates wing-shaped, lateral part directed anteriorly (Viet 1935, figure 115b) ... *A. gracilipes* Piersig
Genital plates not wing-shaped 11
11. Posterior body part truncated, posterior body margin straight (Figure 55) *A. jabiruensis* sp. nov.
Posterior body part not truncated, posterior body margin rounded 12
12. PIV with a large, pronounced anteroventral corner of PIV (Figure 49), genital plates long (> 4 times as long as wide) (Figure 50) *A. anbangbang* sp. nov.
PIV without large, pronounced anteroventral corner, genital plates shorter (< 4 times as long as wide) (Lundblad 1947, figure 48F) *A. forpicatoides* Lundblad
13. PII without a patch of setae 14
PII with a patch of setae 25
14. Dorsal shield covering entire dorsum (Smith and Harvey 1989, figure 2, 3) *A. kitchingi* Smith and Harvey
Dorsal shield smaller than dorsum 15
15. Genital plates long (> 3 times as long as wide) 16
Genital plates short (< 3 times as long as wide) 19
16. PIV very slender, anterior margin of PIV very short (Figure 23), anterior body part dorsally without large humps *A. mantonensis* sp. nov.
PIV of normal shape, anterior body part dorsally with large humps 17
17. Anterior body part dorsally with two large (bifid) humps (Smit 1992, figure 63) *A. roobeeki* Smit
Anterior body part dorsally with three large humps 18
18. Large species ($> 1800 \mu\text{m}$), genital plates widened in the middle (Figure 38) *A. lohmanni* Piersig
Smaller species ($< 1800 \mu\text{m}$), genital plates of equal width over whole length (K. Viets 1955, fig. 31) *A. tricornutus* K. Viets
19. Genital plates reversed bowed (Figure 69) *A. tripartitus* sp. nov.
Genital plates different 20
20. Genital plates close to coxal field 21
Genital plates more or less halfway coxal field and posterior body margin 22
21. Large species ($> 1500 \mu\text{m}$), genital plates not narrowed laterally (Cook 1986, figure 1637) . *A. fissipetiolatus* Lundblad
Small species ($< 900 \mu\text{m}$), genital plates narrowed laterally (Lundblad 1947, figure 49E) *A. tasmanicus* Lundblad
22. Dorsum with a pointed projection (rostrum) ... 23
Dorsum without pointed projection (rostrum) 24
23. Body with distinct posterolateral corners, posterior part of body truncated (K.O. Viets 1984, figure 52) *A. rostratus degeneratus* K.O. Viets
Body without posterolateral corners, posterior body margin rounded (K. Viets 1927, figure 3) *A. rostratus* Daday
24. Genital plates broad (wider than length of genital valve) (Lundblad 1947, figure 50E) *A. novaehollandiae* Lundblad

Genital plates narrow (about half the length of genital valve) (Figure 60)	
..... <i>A. purpureus</i> sp. nov.	
25. Posterior margin of genital plates directing laterally	26
Posterior margin of genital plates sloping posteriorly	27
26. PIV stocky, posterior margin of genital plates with a straight posterior margin (Walter 1929, figure 33, 34) ... <i>A. harpagopalpus</i> Walter	
PIV not stocky and not tapering (Cook 1986, figure 1643), posterior margin of genital plates rounded (Cook 1986, figure 1638)	
..... <i>A. margatellus</i> Cook	
27. Body colour blue	28
Body colour brownish yellow-orange	29
28. Dorsal shield relatively small, ratio body length/length of dorsal shield 1.58–1.70	
..... <i>A. caeruleus</i> sp. nov.	
Dorsal shield relatively large, ratio body length/length of dorsal shield 1.39–1.48	
..... <i>A. thienemanni</i> K.O. Viets	
29. Body length > 1000 µm, genital plates laterally angular (Figure 46)	<i>A. vanderpalae</i> Smit
Body length < 1000 µm, genital plates laterally rounded (Figure 34)	<i>A. gilvus</i> sp. nov.

Manuscript received 15 January 1996; accepted 3 July 1996.

A new species of pliosaurid reptile from the Early Cretaceous Birdrong Sandstone of Western Australia

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Abstract – Of three partial skeletons of small pliosauroid plesiosaurs from near Kalbarri in the Carnarvon Basin, Western Australia, two are described as *Leptocleidus clemai* sp. nov. The third is indeterminate. These constitute the first associated partial skeletons of Mesozoic reptiles recovered from Western Australia, and the first named species of fossil reptile from the State (excluding footprint ichnotaxa). They came from the (upper) glauconitic facies of the Birdrong Sandstone, a late Hauterivian-Barremian (Early Cretaceous) transgressive unit representing a nearshore shallow-marine episode of deposition. Fossil wood associated with the pliosaurs contains fossil pholadid bivalve borings and hyphae of saprophytic fungi. *Leptocleidus* is a small-sized (ca 3 m) genus of pliosauroid plesiosaur which is known from 'Wealden' deposits in England, South Africa and Australia. It retains many characters seen in *Rhomaleosaurus*, a pliosauroid of the English Lias (Hettangian–Toarcian; Early Jurassic). The new species *Leptocleidus clemai* sp. nov. is characterised by being the largest of the known species. Characters of the genus *Leptocleidus* are discussed. A brief review of the distribution of pliosauroids in time shows that the large, open-water, sarcophagous forms appear to have died out at the end of the Turonian and are replaced by the mosasaurs which first appear in the Cenomanian. *Leptocleidus*-like forms seem to have been restricted to inshore habitats.

INTRODUCTION

Pliosauroid plesiosaurs are a characteristic component of many marine faunas throughout the Mesozoic (Brown 1981; Taylor 1992; Cruickshank 1994, 1996a). They represent the top predators of the time and grew to over 14 m in length (*Kronosaurus*, Albion of Queensland). The contrasting plesiosauroids could also grow to extreme lengths, but they were not adapted for the role of sarcophagous predators, being instead pursuers of soft-bodied, or lightly armoured, small prey species (Brown 1981; Massare 1987; Cruickshank and Fordyce, in prep.). The morphological contrast between the superfamilies Pliosauroidae and Plesiosauroidea involves differences in the relative size of their heads, and length of their necks; pliosaurs having relatively large heads and short necks (Tarlo 1960; Taylor 1992; Cruickshank 1994). The morphology of the body and limbs seems not to have varied significantly between plesiosaur and pliosaur, and they all adopted a form of underwater flight as their main form of propulsion (Storrs 1993; Riess and Frey 1991).

Evolutionary trends in the Plesiosauria have been

well documented by Brown (1981), and within the Pliosauroidae there is a conventional view of a general increase in body size through time, a relative increase in head length at the expense of neck length, and an overall decrease in both the number of neck vertebrae and the length of individual centra (Brown 1981; Tarlo 1960). However *Leptocleidus*-like pliosauroids seem not to follow these trends, and keep a neck vertebral count of near 30, do not reduce the lengths of the centra, and have a small body size (ca 3 m). Much of their anatomy is very close to that of the genus *Rhomaleosaurus*, the 5.0 m long top predator of the European Lias (Early Jurassic) (Taylor 1992; Cruickshank, 1996a).

Plesiosaurs have been known from Australia for a number of years (Molnar 1991), but the record in Western Australia is not so complete (e.g., Teichert and Matheson 1944; Long 1993) and the material reported here adds significantly to the knowledge of distribution of these animals in the Australian Cretaceous. Over several collecting expeditions from late 1992 to 1994, sponsored by Mr John Clema and Forrestania Gold Pty Ltd, the remains of three pliosauroid plesiosaurs were

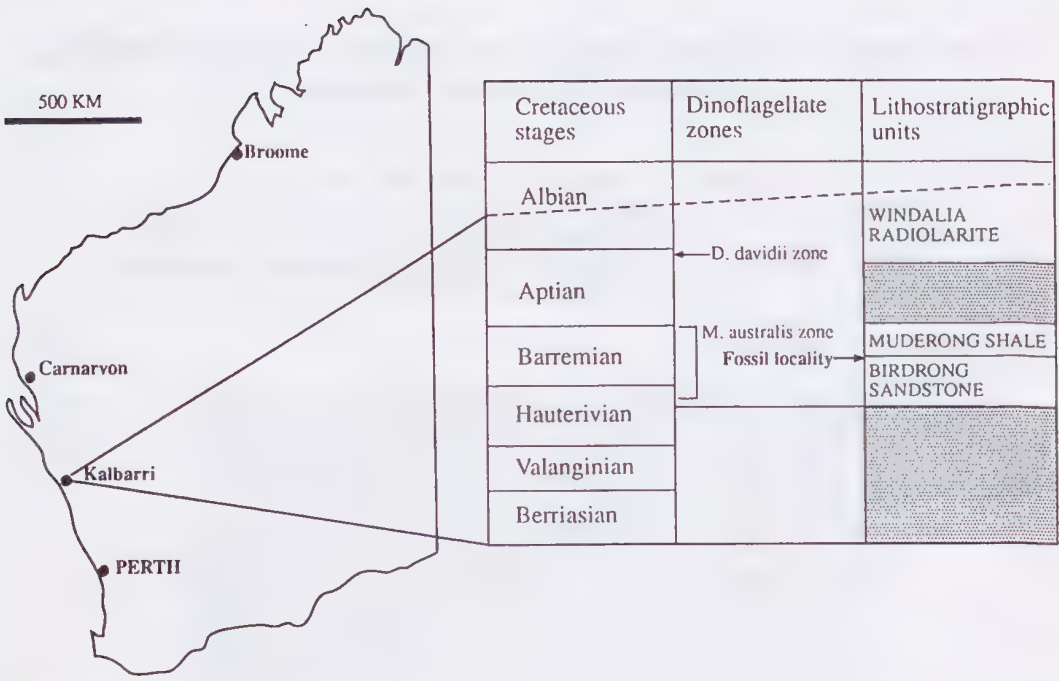


Figure 1 Locality and stratigraphic setting of the pliosauurs from near Kalbarri, Carnarvon Basin, Western Australia. Scale bar =500 km

recovered from the Birdrong Sandstone outcrop near Kalbarri in the Carnarvon Basin, Western Australia and isolated sauropterygian remains were also recovered from outcrops in the northern Carnarvon Basin, near Coral Bay (McLoughlin *et al.* 1995; Hocking *et al.* 1987) (Figure 1). The skeletons all lack skull material, but are well enough preserved to be ascribed to a new species of the 'Wealden' (Early Cretaceous) genus *Leptocleidus* Andrews 1922 on size differences of their postcranial bones. This genus is known from England and South Africa (Andrews 1911; 1922; Cruickshank 1997), and probably from the Albian/Aptian of Coober Pedy, Australia (Schroeder in prep.), although the new species described herein becomes the first species of the genus to be formally named ed from Australia.

Incorporated in the material described below are a few anomalous bones which do not seem to be part of plesiosaurian skeletons. One (found near the specimen may be a mid-caudal vertebra from a theropod dinosaur, and three others, from another skeleton (WAM 92.8.1) could possibly be from a jaw too big to belong to a pliosauur of the presumed size of the species described here. The purpose of this paper is put these discoveries on record, pending a fuller review of other *Leptocleidus* occurrences in the Early Cretaceous.

The Birdrong Sandstone

In the Carnarvon Basin the Cretaceous rocks generally lie on an erosion surface cut into Permian strata (Figure 1), although in Kalbarri the Cretaceous sequence rests unconformably above the ?Silurian Tumblagooda Sandstone. The Birdrong Sandstone is the basal unit and is ca 10 m thick, being overlain by 56 m of the Muderong Shale, a carbonaceous mudstone-siltstone. The Birdrong Sandstone belongs to the *Muderongia australis* Zone of late Hauterivian-Barremian age, as does the lower part of the Muderong Shale (McLaughlin *et al.* 1994). The age of the upper Muderong Shale is uncertain, as is the age of the 10 m thick sandstone unit which separates the Muderong Shale from the late Aptian Windalia Radiolite. Changes in sediment composition, palynomorph assemblages and forminiferal biofacies reflect retrogradation of marine facies during deposition of the Birdrong Sandstone and lowermost Muderong Shale, followed by aggradation through most of the Muderong Shale, with a maximum water depth of never more than 50 m. At its type section on Mardathuna Station, northeast of Carnarvon, the Birdrong Sandstone begins with a fluvial phase of deposition, followed by deltaic and shallow marine facies (Hocking *et al.* 1987).



Figure 2 Attempted reconstruction of the skeleton of *Leptocleidus clemai* sp. nov. showing relative completeness of remains so far recovered shown in black. Skull and other proportions are based on *Peloneustes* and *Leptocleidus* sp.

The sequence reflects a transgressive pulse that was part of the progressive submergence of vast areas of the Australian continent during the Early Cretaceous (Dettmann *et al.* 1992). This late Hauterivian-Barremian transgressive pulse is recognized in widely separated basins in Australia, and may represent a synchronous continent-wide sea-level rise. A similar sea-level rise is seen in the Algoa Basin (and other smaller basins) on the South African south-east coast, where *Leptocleidus capensis* has been recovered from Valanginian inshore deposits (Cruickshank 1997; McLachlan and McMillan 1977; McMillan in prep.). The earlier date for the South African deposits reflects a probable earlier phase of the break-up of (east) Gondwana.

Institutional abbreviations used in this paper: WAM – fossil collections of the Department of Earth and Planetary Sciences; SAM – fossil collections in the Division of Palaeontology, South African Museum; NHM – fossil collections in the Palaeontology Department, The Natural History Museum, London.

MATERIAL AND METHODS

(a) WAM 92.8.1–1 to 68. The first specimen to be recovered comprises numerous vertebral centra, left and right femora, right tibia and fibula, left tibia, a possible partial ulna, base and part of the shaft of a left ilium, a badly damaged head of a humerus, broken parts of the pectoral girdle (scapula?) and pelvic girdle elements, part of a neural arch, and several rib fragments. The centra are distributed as follows: 11 cervical, 3 pectorals, 17 dorsal, 2 sacral(?), 5 caudals and one so badly preserved that its position is not identifiable, but it is possibly a dorsal. In addition to the elements which can be confidently assigned to a pliosaur, there are three heavily ossified portions of what appear to be the mid-part of a lower jaw, lacking teeth, which if reconstructed would be far too big

for the assumed size of this pliosaur.

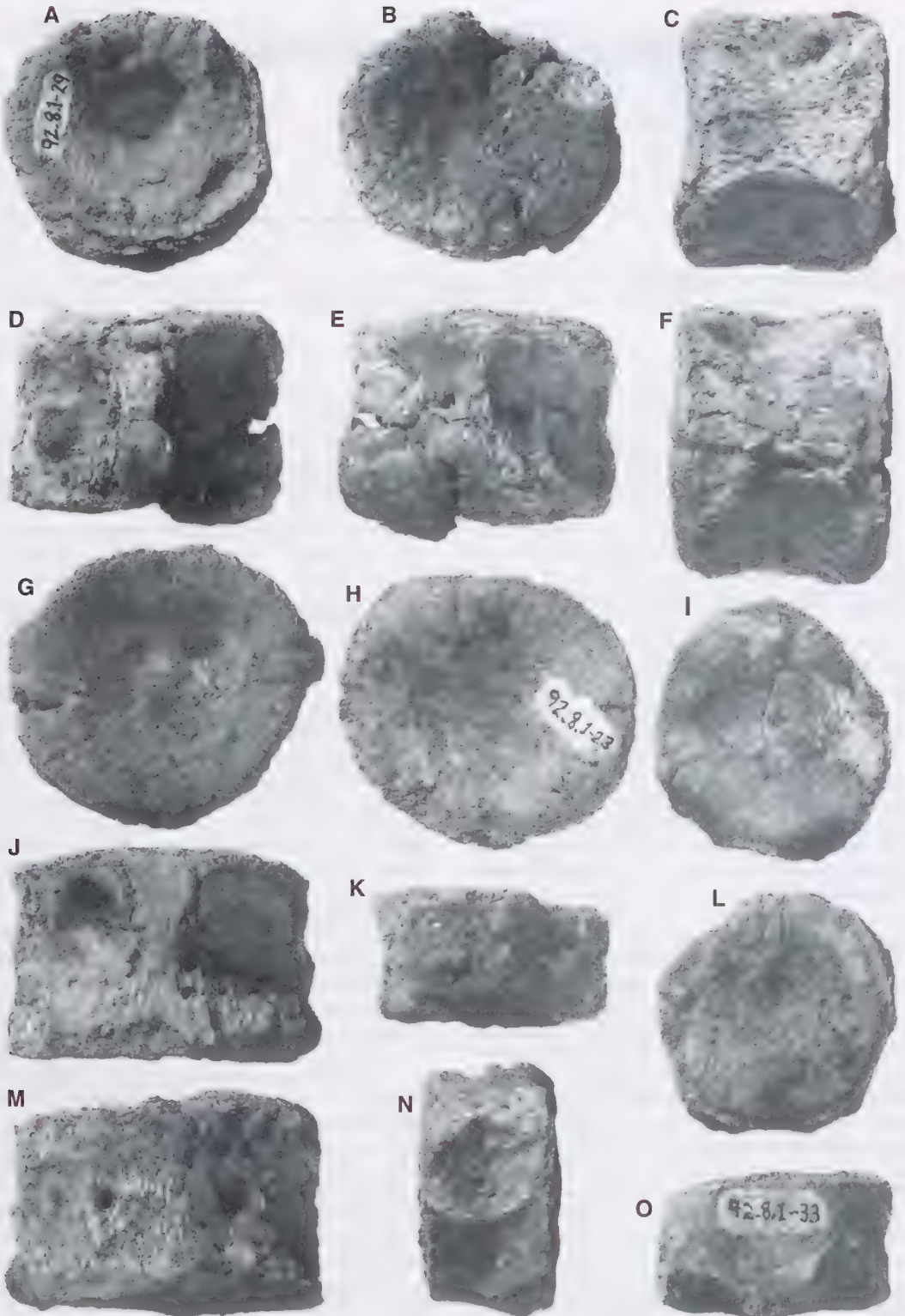
(b) WAM 94.1.6–1 to 100. The second best preserved of the three. It comprises a length of the vertebral column encased in a nodule extending over about 15 vertebrae, and the following individual bones which can be identified: 9 cervical vertebrae, about 20 dorsal vertebrae as well as some fragments, 4 sacral, one caudal, a fragment of scapula, portions of two ilia and, a piece of pubis, two humeri, one possible phalanx, an unidentifiable epipodial and five pieces of rib, apart from some very poorly preserved lengths of rib still in the nodule.

A very badly preserved, but elongate, centrum found near the specimen is not plesiosaurian but is from the mid-caudal region of a medium-sized theropod dinosaur, and is described elsewhere (Long and Cruickshank 1997).

(c) WAM 96.5.2. The material comprising this specimen is badly preserved and mostly unidentifiable as to taxon, except for some dorsal vertebrae which appear to be similar in size and proportion to those of the other two specimens. It is noted here only to complete the record.

Figure 2 shows a generalised pliosaurid skeleton with the known remains from *Leptocleidus clemai* sp. nov. shaded in black, indicating the degree of completeness from the combined two partial skeletons.

Excavation and preparation procedures used on this material were standard, using pneumatic airscribes and manual chisels to clear the friable sandy matrix and the thin layer of encrusting iron-rich cementing minerals from the specimens. Mends were made with proprietary organic glues dissolved in acetone, and therefore reversible, except for the joining together of the thicker bones (eg the humeri) in which epoxy resins were used. Some portions of the specimens were transported in plaster jackets and extracted from the matrix in the laboratory. Measurements were made to the nearest 0.1 mm, using sliding vernier calipers.



SYSTEMATIC PALAEOONTOLOGY

Class Reptilia

Subclass Sauropterygia Owen, 1860

Order Plesiosauroidea de Blainville, 1835

Superfamily Pliosauroidae (Gray, 1825) Welles, 1943

Family Pliosauridae Seeley, 1874

Genus *Leptocleidus* Andrews, 1922

Type species

Leptocleidus superstes Andrews, 1922

Emended diagnosis

Leptocleidus can be defined as a small genus of pliosauroid possessing cranial and postcranial characters of a conservative kind, being in many ways no more derived than the Liassic (Early Jurassic) genera *Eurycleidus* and *Rhomaleosaurus* (Andrews 1922; Cruickshank 1994, 1996a; Taylor 1992). Skull triangular in outline, with a prominent midnasal ridge which merges with the parasagittal crest, flanked by deep grooves or depressions which in turn cause the orbital rims to stand up from the general profile of the skull. Compared with *Rhomaleosaurus* the tooth count is reduced, to 21 positions on each side of the upper jaw (5 in each premaxilla + 16 in each maxilla), compared with at least 27 in the upper jaw of *R. megacephalus* (Cruickshank 1994), and a similar number in *R. zetlandicus* (Taylor 1992; Cruickshank 1996a). No complete jaw is known for the genus, but an estimated tooth count is 35 (*L. capensis*), at the lower end of the known range for pliosaurids. A spatulate lower jaw symphysis with five pairs of teeth is assumed for *L. capensis* (Cruickshank 1997). *Leptocleidus* possesses a dorsomedially directed trough on the prearticular and adjacent bones of the lower jaw, similar to *Rhomaleosaurus*. Pectoral girdle primitive, having large clavicles and interclavicles and small scapulae (Andrews 1922); humerus has a very much more symmetrical (fan-shaped) distal end, in contrast to *Rhomaleosaurus* which has the humerus gently curved posteriorly (Cruickshank 1996a; in press). None of the vertebrae are compressed, cervicals being spool-shaped with the neural arches relatively large when compared with, for example, *Pliosaurus brachyspondylus* (Taylor and Cruickshank 1993). Cervical vertebral count in excess of 13. *Leptocleidus* differs from early forms in one other feature in

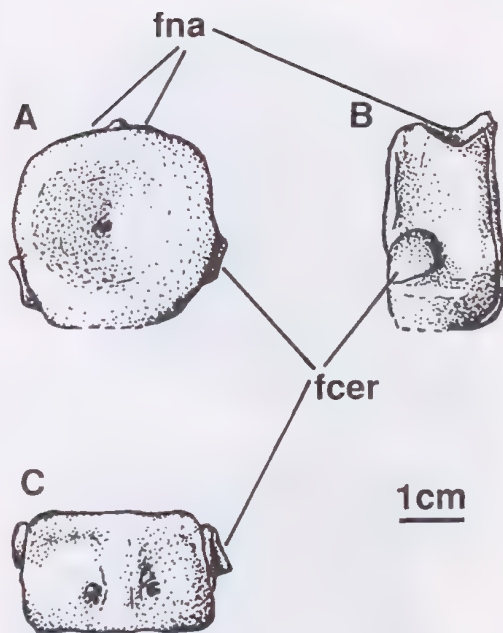


Figure 4 *Leptocleidus clemai* sp. nov. Anterior cervical vertebra of WAM 94.1.6–64, in anterior (A), left lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fcer, attachment of cervical rib.

possessing a forwardly-pointing expansion ('cockscorn') on the squamosal mid-line, at the rear of the parasagittal crest, very similar to that seen in Late Cretaceous Polycotylidae (Welles 1962; Thurmond 1968).

Remarks

The genus has been redefined in the light of new material plus observations of undescribed specimens made by one of us (ARIC). We consider it important to include this here as further new specimens of the genus have been uncovered throughout eastern Australia which we anticipate will be described in the near future. It should be noted that jaw morphology and possibly the humerus and cervical vertebral morphology and count follow closely those of Early Jurassic genera such as *Rhomaleosaurus*. This is unusual in that it is usually recognised that by the Late Jurassic pliosaurs reduced their neck vertebral count to 13 highly compressed disc-like centra. The presence

Figure 3 *Leptocleidus clemai* sp. nov. Holotype 92.8.1. A–E, cervical vertebra 92.8.1–29, seen in anterior (A), posterior (B), left lateral (C), dorsal (D) and ventral (E) views. F–H, J, M, postcervical vertebra, 92.8.1–23 in left lateral (F), anterior (G), posterior (H), dorsal (J) and ventral (M) views. I, K, L, N, O, caudal vertebra 92.8.1–33 in posterior (I), dorsal (K), anterior (L), left lateral (N) and ventral (O) views. All shown natural size.

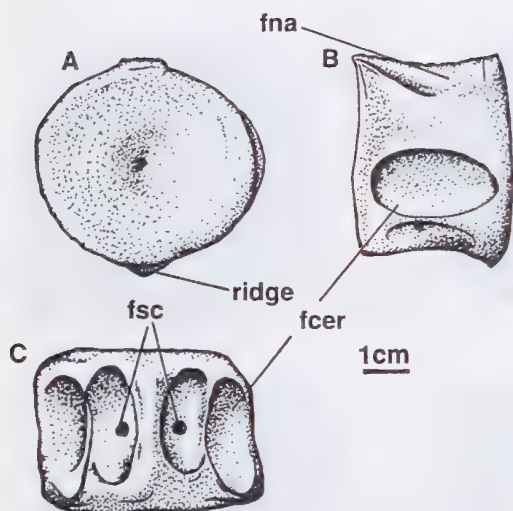


Figure 5 *Leptocleidus clemai* sp. nov. Mid cervical vertebra of WAM 92.6.1–30 in anterior (A), lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fcer, attachment of cervical rib; fsc, sub-central foramina.

of a dorsomedian trough on the inner surface of the articular region of the lower jaw was thought to be an autapomorphy of *Rhomaleosaurus* (European Lias).

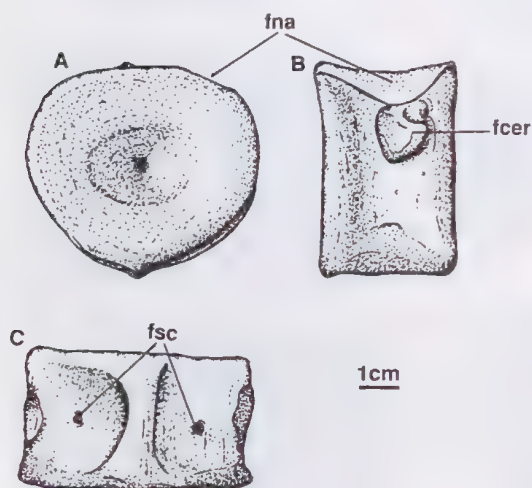


Figure 6 *Leptocleidus clemai* sp. nov. Posterior cervical vertebra of WAM 92.8.1–20 in anterior (A), lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations as for Figure 5.

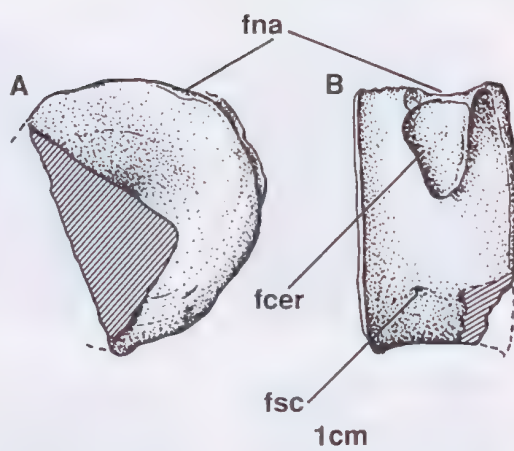


Figure 7 *Leptocleidus clemai* sp. nov. Posterior cervical vertebra of WAM 94.1.6 – 60 in anterior (A) and lateral (B) views. Scale bar = 1 cm. Abbreviations as for Figure 5.

Leptocleidus clemai sp. nov.

Figures 3–16

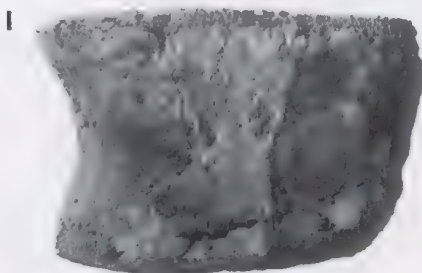
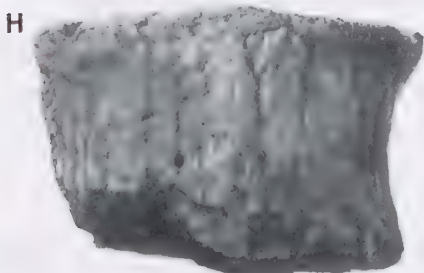
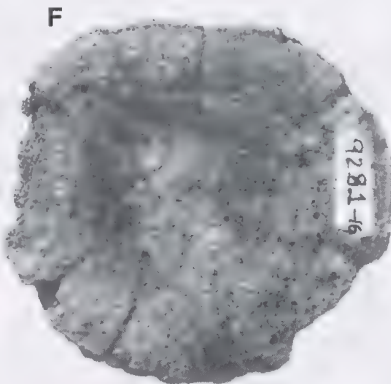
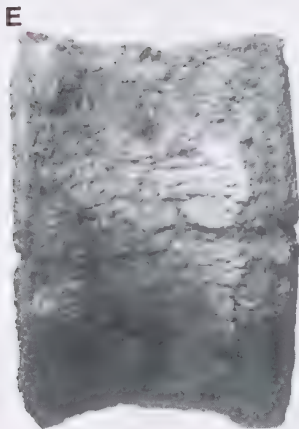
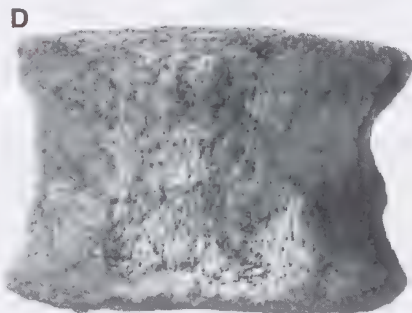
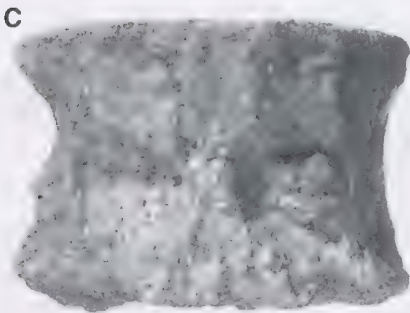
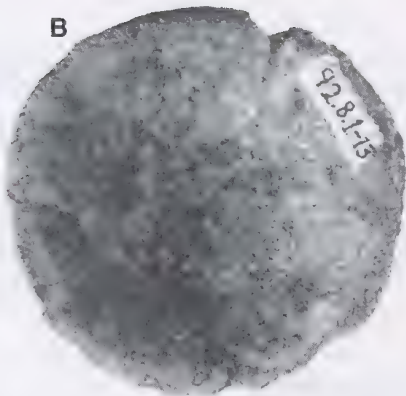
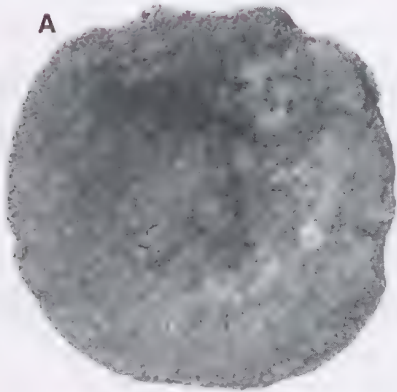
Type specimen

Holotype is WAM 92.8.1–1 to 68 (Figs. 3, 5, 6, 8–12, 13A, C–E, 14, 16), a partial skeleton comprising right femur (92.8.1–2), part of tibia (92.8.1–3), parts of the left femur (92.8.1–4), possible fragments of lower jaw, lacking teeth, (92.8.1–5A, B), pelvic girdle element (92.8.1–7), part of a propodial head (92.8.1–8), part of left ilium (92.8.1–9), portion of ilium shaft (92.8.1–56), lower jaw? fragment (92.8.1–57), ?part of scapula (92.8.1–58), various bone fragments and parts of neural arches (92.8.1–59 to 92.8.1–64), left ulna (92.8.1–65), right ulna (92.8.1–66), right radius (92.8.1–67) part of propodial? (92.8.1–68) and some 45 vertebrae (92.8.1–10 to 92.8.1–55). All specimens of *Leptocleidus clemai* sp. nov. are housed in the palaeontological collections of the Western Australian Museum.

Horizon and locality

The exact localities have been kept private at a request from the property manager, but they are recorded in the Department of Earth and Planetary Sciences locality register (within the Western Australian Museum). Upper metre of the Birdrong Sandstone, Early Cretaceous (Hauterivian–Barremian), Kalbarri region, Western Australia.

Figure 8 *Leptocleidus clemai* sp. nov., WAM 92.8.1, dorsal vertebrae. A–E, 92.8.1–13 in posterior (A), anterior (B), dorsal (C), ventral (D) and right lateral (E) views. F–I, 92.8.1–16 in anterior (F), left lateral (G), ventral (H) and dorsal (I) views. All shown natural size.



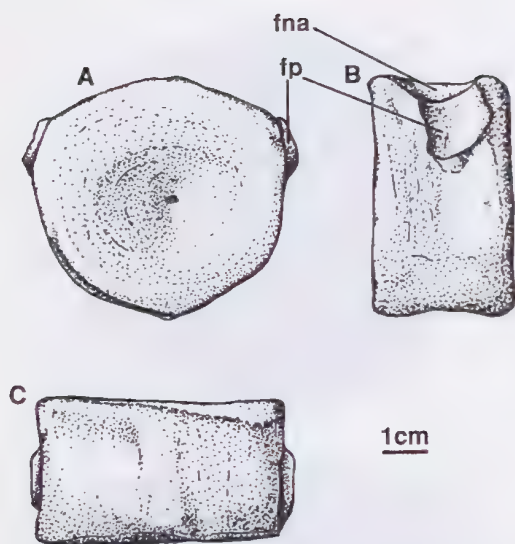


Figure 9 *Leptocleidus clemat* sp. nov. First pectoral vertebra of WAM 92.6.1-21 in anterior (A), left lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fp, pectoral rib attachment.

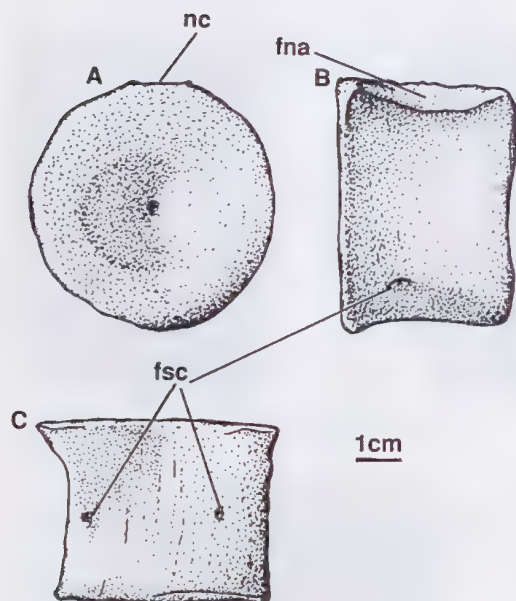


Figure 10 *Leptocleidus clemat* sp. nov. Dorsal vertebra of WAM 92.8.1-14 in anterior (A), left lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fsc, sub-central foramina; nc, fossa for neural cord.

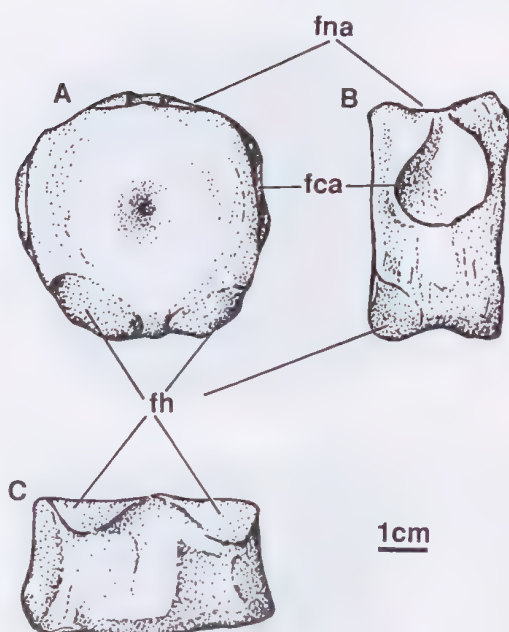


Figure 11 *Leptocleidus clemat* sp. nov. Caudal vertebra of WAM 92.8.1-54 in anterior (A), left lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fca, fossae for transverse ribs, fh, fossae for attachment of chevron bones, fna, fossae for neural arch attachment.

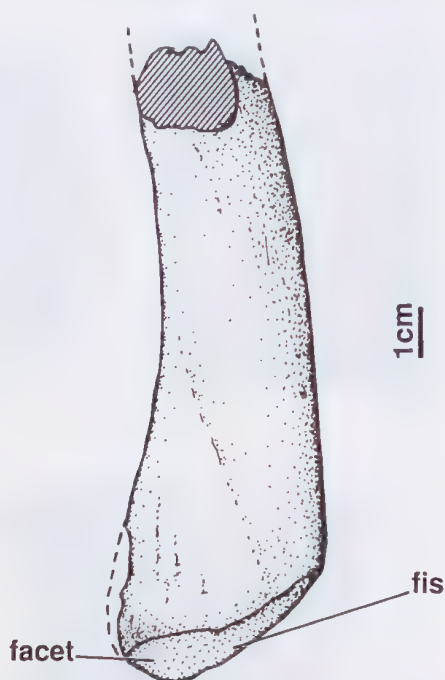


Figure 12 *Leptocleidus clemat* sp. nov. Left ilium of WAM 92.8.1-9. Scale bar = 1 cm. Abbreviations: fis, median fissure of ilia.

Referred material

WAM 94.1.6–1 to 100 (94.1.6–1 through to 94.1.6–94), a less well preserved partial skeleton, dimensionally very similar, approximately 100 associated, partially articulated bones found underneath a single large concretion (Figures 4, 7, 13B, 15).

Etymology

In honour of Mr John M. Clema of Perth, Western Australia, who has generously supported and assisted in fossil collecting expeditions by the Western Australian Museum over the years 1993–1995.

Diagnosis

A species of *Leptocleidus* whose vertebrae are at least 30% greater in linear dimensions than those of either *L. superstes* or *L. capensis*, and whose propodials are 10% – 15% greater in size (WAM 92.8.1–2, femur 274 mm long). The epipodials show a derived state when compared with *L. capensis* in being wider than long.

Description of material

Holotype (WAM 92.8.1, Figs. 3, 5, 6, 8–12, 13A, C–E, 14, 16).

Distinguishing between the various parts of the vertebral column was difficult in both the principal specimens reported here due to the poor state of preservation and fracturing of vertebrae. It has been assumed that the distinction between cervical and sacral centra is that the former have a mid-ventral keel, and prominent sub-central foramina in addition to the facets for the cervical ribs, which possibly could be confused with one or other of the sacral series. Pectoral centra do not have the

prominent mid-ventral keel, but the most anterior pectoral centrum has a large part of its rib facet still on the centrum, which in a poorly preserved specimen also might cause confusion with one of the sacral series. Caudal centra, apart from the very first few, have haemal facets and should not be confused with any others. Dorsal centra do not have rib facets and often do not have prominent sub-central foramina nor mid-ventral keels. They are often very much more robust than others in the vertebral column.

All the centra are spool-shaped (Figures 3–11), are concave on their faces, and none has its neural arch in position. Mostly the evidence points to the bases of the neural arches having come cleanly away from the centra, indicating lack of fusion and hence a sub-adult (‘juvenile’) age for the specimen. The centrum with the greatest length is a dorsal at about 42.4 mm. The shortest is a caudal at 22.5 mm. All centrum widths are significantly greater than their lengths, and also greater than, or sub-equal to their heights. The cervical vertebrae are not markedly shortened (Figures 3A–E). They are only slightly shorter than the pectorals, but more so when compared with the dorsals (Table 1). However the overall impression is a vertebral column of uniformly proportioned centra, as far back as the caudal series, when some compression is seen. This is a markedly primitive vertebral column for a Cretaceous pliosaur (Andrews 1922; Brown 1981; Tarlo 1960; Taylor and Cruickshank 1993), but seems to be very similar to the other species of *Leptocleidus* (*L. capensis* (Andrews 1911) and *L. superstes* Andrews 1922), differing only in the overall size of the individual elements.

Of the femora, the right is best preserved (Figs 13A, 14). Its dimensions are 274.0 mm long, 76.3 mm across the head and 123.4 mm wide distally.

Table 1 Some measurements of *Leptocleidus* specimens. The vertebral measurements are listed in sequence as ‘Length’, ‘Breadth’ (Width) and ‘Height’. The limb bone measurements are overall length, width of head in plane of the distal expansion, and width of distal end.

Identity	<i>L. superstes</i> BMNH R4824			<i>L. capensis</i> SAM K-5822			<i>L. clemai</i> WAM 92.8.1			<i>L. clemai</i> WAM 94.1.6		
post cervical	25	38	30	19	30	35	35.4	63.3	55.2	39.4	56	55.5
ant cervical	22	25	25							20	34.2	30.7
mid cervical				25	36	31	35	48.9	44.6			
post cervical	25	38	30	19	30	35	35.4	63.3	55.2	39.4	56	55.5
	32	43	40	21	33	27	35.6	62.3	54.7			
dorsal	31	55	48	32	50	41	40.5	52.6	52.1	32.5	55.8	49.5
				28	46	41	40	60.9	58.3	35	58	53.5
							41.9	63.9	64.1	41.2	73.1	68
l.humerus	245	60	124									
r.humerus										270	68.2	127.6
r.femur							274	76.3	123.4			



Figure 13 *Leptocleidus clemati* sp. nov., A, femur in dorsal view, WAM 92.8.1-2, x0.5. B, lower part of left ilium, 92.8.1-9, x1. C, humerus in dorsal view, WAM 94.1.6-95, x0.5. D, tibia, 92.8.1-66 in dorsal view, x1; E, fibula, 92.8.1-67, in dorsal view, x1.

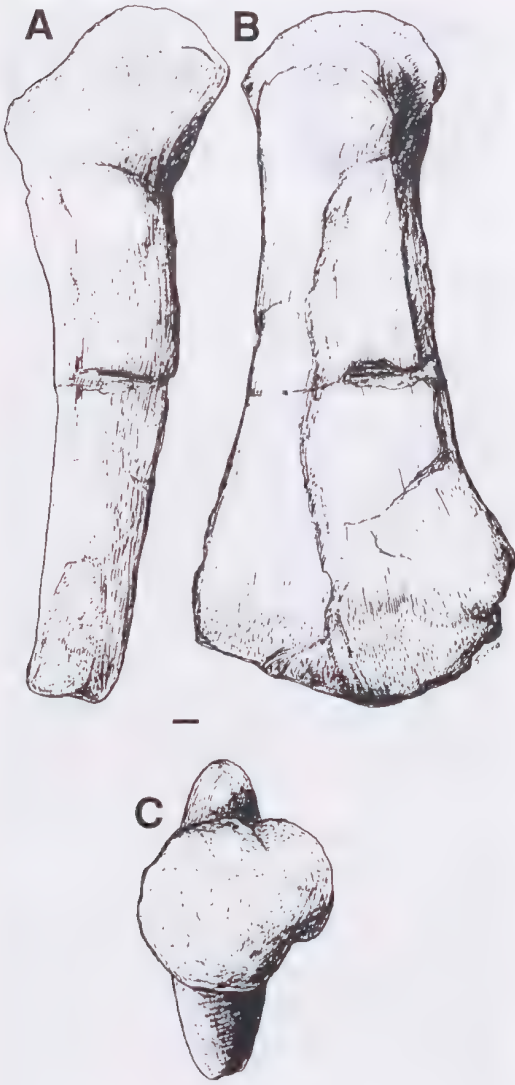


Figure 14 *Leptocleidus clemai* sp. nov., WAM 92.8.1–2, femur, in anterior (A), dorsal (B) and proximal (C) views.

There is a notch developed between the tibia and fibula, which are wider than long (Figure 16). The ilium (Figures 12, 13C) is well ossified, but its distal end is not preserved.

WAM 94.1.6–1 to 100 (Figs 4, 7, 13C, 14)

The second specimen seems to be identical with the foregoing, so little of the corresponding material is illustrated. The vertebrae range in overall length from 20.0 mm for an anterior cervical (Figure 4) to 41.2 mm for a dorsal centrum (Figure 11). Sacral vertebrae range from 28.0 mm

to 38.2 mm, and cervicals range in length up to 39.7 mm. These sizes coincide with those for WAM 92.8.1 with the exception of the anterior cervical vertebra, which is from a region of the neck much further forward than in WAM 92.8.1.

The complete right humerus of WAM 94.1.6 (Figures 13C, 15) is 270 mm long, 68.2 mm across the head and 127.4 mm across the distal expansion (Table 1). It does not have the preaxial expansion seen in other late pliosaurs, and is reminiscent of the humeri of Early Jurassic plesiosaurs (Cruickshank 1996b).

These specimens represent two sub-adult small pliosaurids with an estimated maximum length of 2.5 to 3 m. (based on proportions of *Rhomaleosaurus*), from shallow marine waters of the Early Cretaceous of Western Australia, which vary from other known members of the genus *Leptocleidus* only in their greater size.

DISCUSSION

Maturity of specimens

A question as to whether the specimens described here are juvenile or not deserves comment. The limb bones are all very well ossified and do not give the impression of being from young animals. However the neural arches of the two other species of *Leptocleidus* are firmly fused to their centra, and certainly these two specimens must be regarded as 'adult'. Notwithstanding these observations, the specimen of *Pliosaurus brachyspondylus* described by Taylor and Cruickshank (1993) is a very large animal (skull length ca 2m), the skull sutures were well fused, and yet the cervical vertebrae did not have their neural arches fused. It is unlikely that an observer would have called that animal, if seen alive, 'juvenile'. We prefer to regard these specimens from the Birdrong Sandstone as being sub-adult, probably being close to fully grown when they died.

Distribution of 'primitive' pliosauroids

Leptocleidids (Early Cretaceous) seem to be very similar to, if smaller than, rhomaleosaurid (Early Jurassic) pliosaurs. An ancestor-descendant relationship can be confidently inferred for them (Cruickshank 1996a). They seem to have been inhabitants of the close-inshore, marine, environments in a manner similar to modern sea-lions, and may have moved to this environment under pressure from the later, larger, Jurassic forms such as *Liopleurodon*, *Simolestes*, *Pliosaurus* and *Peloneustes* (Andrews 1910–1913; Taylor and Cruickshank 1993). These large forms, in the Cretaceous, are typified by the genus *Kronosaurus*, but which did not survive beyond the Turonian,

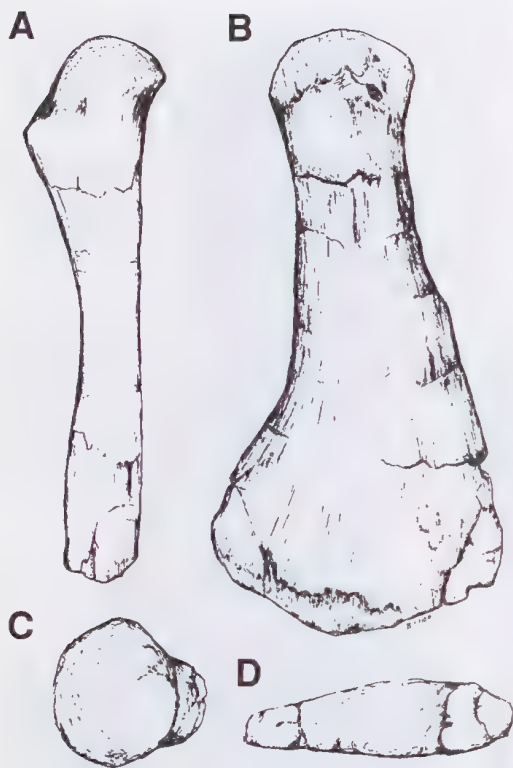


Figure 15 *Leptocleidus clemat* sp. nov., WAM 94.1.6-95, humerus in anterior (A), dorsal (B), proximal (C) and distal (D) views.

leaving only the polycotyloid pliosaurs as the last remaining representatives of the Pliosauroidae (Benton 1993). It is worth noting in this respect that the first mosasaurs are known from the

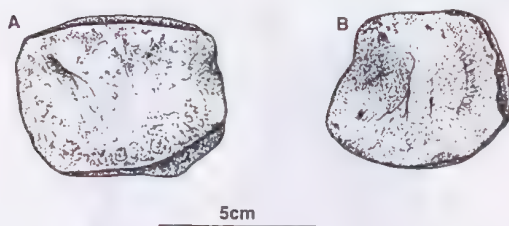


Figure 16 *Leptocleidus clemat* sp. nov. A, WAM 92.8.1-66, right tibia in dorsal view. B, WAM 92.6.1-67, right fibula of in dorsal view. Scale bar = 1 cm.

Cenomanian, about the same time as ichthyosaurs become extinct worldwide (Benton 1993), and may have been able to out-compete the pliosaurs in some way not yet known. Maybe they were the more capable swimmers (Massare 1988). They certainly had a very different feeding mechanism. But the puzzle is, if the large pliosaurs disappeared, then why not the cryptocleidids and elasmosaurs? Both of these families survived right to the end of Cretaceous times (Cruickshank and Fordyce in prep.).

Leptocleidids are known to occur in association with other shallow marine to fluvial vertebrate assemblages. In the English Wealden, a lagoonal deposit, remains of *L. superstes* occur with terrestrial dinosaurs (e.g., *Hypsilophodon*, *Iguanodon*, *Baryonyx*). In South Africa *L. capensis* occurs in an inshore marine to lagoonal deposit whose foraminifera have a heavy nonmarine imprint, and remains of terrestrial dinosaurs and wood also occur in close association. In South Australia the Early Cretaceous deposits of Coober Pedy and Andamooka containing *Leptocleidus* sp. (the famous "Eric" specimen at the Australian Museum, Sydney) also yield the remains of terrestrial

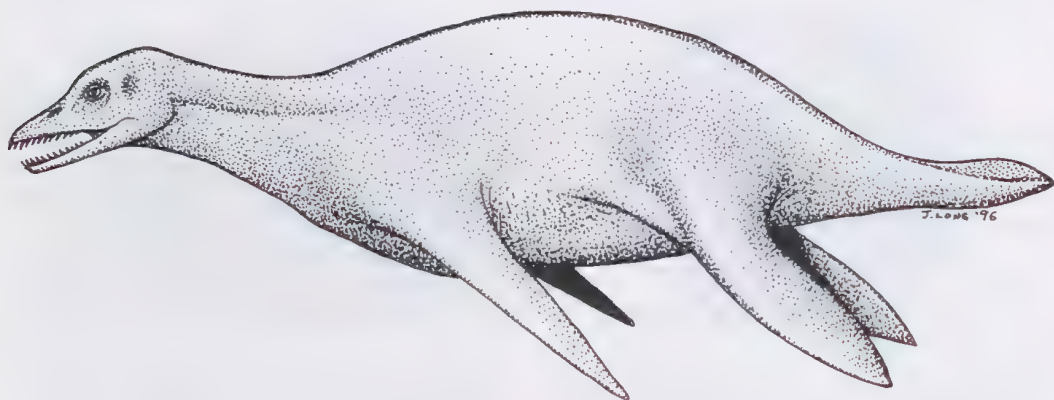


Figure 17 Attempted reconstruction of *Leptocleidus clemat* sp. nov. by J. Long.

dinosaurs (e.g., *Kukuru kujani* Long 1993) together with fossilised wood. Thus the noted occurrence of a theropod dinosaur bone found near WAM 986.8.1 along with the high abundance of fossilised wood from the Birdrong Sandstone strongly suggests that this unit would be a potentially good target to direct future exploration for dinosaurs.

SUMMARY AND CONCLUSIONS

Two partial skeletons from the Early Cretaceous Birdrong Sandstone of Western Australia are ascribed to the pliosauroid genus *Leptocleidus* as *L. clemai* sp.nov. *Leptocleidus* is a small-sized genus (under 4 m), known from the Early Cretaceous of England, South Africa and Australia. It seems to have occupied a close inshore or shallow marine habitat, as opposed to the more typical open marine habitat of the larger forms such as *Kronosaurus*. *Leptocleidus* is close to, but smaller than, the Early Jurassic genus *Rhomaleosaurus*. It may be ancestral to the later Cretaceous forms known as the Polycotylidae. It is noted that the large pliosauroids died out by the Turonian and were replaced by the mosasaurs, leaving the polycotylids as the last remaining pliosaurs. An anomaly is that the pliosauroid pliosaurs continued very successfully as predators on small and soft-bodied marine animals until the end of the Mesozoic.

ACKNOWLEDGEMENTS

We thank the generous sponsorship of Mr John Clema, of Forrestfield, and Forrestania Gold Pty Ltd, for grants fully supporting field exploration of the Birdrong Sandstone over three field seasons (1992–1994), and partial funding of preparation of specimens. Many helpers assisted in the field excavations or offered helpful discussion of the age of the sites, so we extend our sincere thanks to Greg Milnar, Ian Copp and Glynn Ellis, Kristine Brimmell, David Haig, Alex Ritchie, Mikael Siverson, Alex Baynes and John Clema. We thank Kristine Brimmell for the photography of the specimens, Jenny Bevan for preparation of specimens, and Danielle Hendricks for drafting assistance. ARIC is indebted to the Royal Society of London for travel support, and to the three women in his life for encouragement and help in undertaking a long research visit to the antipodes in early 1996.

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Manuscript received 14 August 1996; accepted 3 December 1996.

Two new cuttlefishes (Cephalopoda: Sepiidae) from the North West Shelf, and a redescription of *Sepia sulcata* Hoyle, 1885

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Abstract – Two new cuttlefishes (Cephalopoda : Sepiidae), *Sepia plana* sp. nov. and *Sepia senta* sp. nov., are described, and a third species, *Sepia sulcata* Hoyle, 1885, is redescribed from the type and new Australian material. The three species are found in the Indian Ocean off northwestern Australia at depths between 505–150 m. *Sepia plana* is found in the deeper end of this range, between 505–396 m. *Sepia senta* and *Sepia sulcata* have been collected at 426–256 m, and 404–150 m respectively. *Sepia sulcata* Hoyle was known previously from a single male collected off the Ki Islands in the Arafura Sea.

INTRODUCTION

The genus *Sepia* includes approximately 100 species (Khromov *et al.* in press), and is the largest of three genera within the family Sepiidae. In the genus *Sepia*, 26 species are found in Australian waters, and 21 are endemic to this country (Lu in press, a).

As part of a broader study to revise the cuttlefish fauna of Australia, two new species from the North West Shelf, *Sepia plana* sp. nov., and *Sepia senta* sp. nov. are described in this paper. In addition, *Sepia sulcata* Hoyle, 1885 is redescribed based on new material from the North West Shelf. The latter species was known previously only from a single male specimen collected off the Ki Islands in the Arafura Sea in 1874, and described later by Hoyle (1885). Khromov *et al.* (in press) has described its status as “probably valid, but insufficiently described”. Conspecificity of the Australian animals with *S. sulcata* was confirmed by comparison with the type specimen. While the type, an immature male, differs from the more mature Australian males in the degree of modification of the hectocotylus, most other traits agree between the North West Shelf specimens and *S. sulcata*.

This finding confirms the status of *S. sulcata* as valid and extends the distribution of the species to include northwestern Australia. The redescription of this species from the type and additional material provides information which previously was not known on females and mature males of this species.

MATERIALS AND METHODS

This study is based on specimens held in various

museums. All material studied is listed in the *Material Examined* sections given with each species description. Institutional acronyms used throughout the paper are: BMNH – The Natural History Museum, London, United Kingdom; CSIRO – Commonwealth Scientific and Industrial Research Organisation, Australia; MV – Museum of Victoria, Melbourne, Australia and WAM – Western Australian Museum, Perth, Australia. Other abbreviations: coll. – collected, E – east, fms – fathoms, F – female, FV – Fisheries Vessel, Is. – Island, J – juvenile, m – metres, M – male, mm – millimetres, N – north, NW – northwest, NNW – north northwest, RV – research vessel, S – south, W – west, WNW – west northwest.

Measurements and indices used throughout this paper are primarily those given in Roper and Voss (1983), using dorsal mantle length (ML) as a size standard. Some additional measurements are used, and these with the definitions listed by Roper and Voss (1983) are given in Table 1. Parts of the club and arm sucker rims are described using the terminology of Nixon and Dilly (1977), and nomenclature for radulae follows Nixon (1995). Beaks were described following Clarke (1986). Diagrammatic illustrations of measurements and terminology used for particular structures are shown in Figure 1. With respect to the arrangement of arm and club suckers, the term ‘row’ refers to suckers positioned perpendicular to the longitudinal axis of the arm or club. ‘Series’ refer to those positioned parallel to the longitudinal axis of the arm or club.

Measurements were made either using dial callipers, or an eyepiece micrometer attached to a stereo microscope and (where possible) are given for 10 preserved specimens of each sex for each

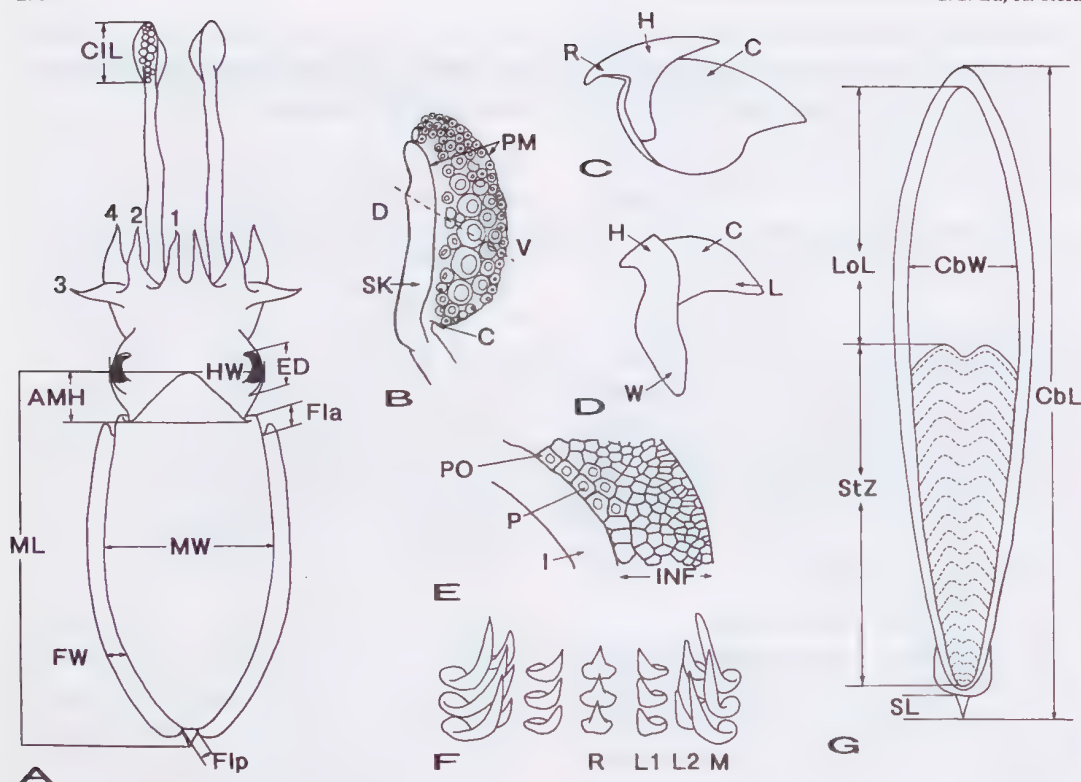


Figure 1 A-F, Measurements and Terminology; A, whole animal dorsal view (for abbreviations and definitions see Table 1); B, tentacular club (C - carpus, D - dorsal, PM - protective membranes, SK - swimming keel, V - ventral). The number of suckers intersected in an oblique transverse line across the club, shown as a hatched line on this figure, is the Club Row Count (CIRC). In the example illustrated CIRC = 4.; C, upper beak (C - crest, H - hood, R - rostrum); D, lower beak (C - crest, H - hood, L - lateral wall, W - wing); E, arm sucker rim (I - inner ring, INF - infundibulum, PO - polygonal process, P - peg); F, radula (R - rhachidian teeth, L1 - first lateral teeth, L2 - second lateral teeth, M - marginal teeth); G, cuttlebone, ventral view (for abbreviations and definitions, see Table 1). [A and G modified from Roper and Voss (1983) Figure 1].

species. All measurements are expressed in millimetres (mm). Measurements and counts for individual specimens are shown in tables accompanying descriptions. Ranges of arm length indices, arm sucker diameter indices, and arm sucker counts are also presented in tables accompanying descriptions, ranges for all other characters appear in the text. In species descriptions and tables, the range of values for each character are expressed as: minimum - mean - maximum (standard deviation (SD)). Ranges refer only to mature animals, and values for each sex are given separately. Numbers shown in bold with the range of measurements for mantle length indicate the upper size limit for each sex (numbers appear after the upper limit of the range when the largest specimens were not necessarily among the 10 specimens selected for detailed examination and measurement for all characters).

Measurements for structures which were clearly distorted or broken were not attempted, and these, in addition to missing values, appear as a dash (-) in the tables. Ranges for specific character traits given with each species description do not, therefore, always refer to the total number of specimens examined for each species.

For scanning electron microscopy, arm and club suckers were removed from the middle of designated arms and the tentacular club, and dehydrated in an ethanol series through to 100% ethanol then air dried. Radulae and beaks were dissected from the buccal mass, and soaked for approximately half hour in a warm, saturated potassium hydroxide solution, then radulae were cleaned using forceps and a fine brush. In all cases, the new, unused portion of the radula was examined. All prepared material was mounted, gold coated and examined in a JSM 6400 (Japan

Table 1 Description of measurements and counts. Definitions largely follow Roper and Voss (1983). New or modified definitions are indicated by an asterisk (*). Indices (shown in square brackets) are calculated by dividing each measure by mantle length or, for cuttlebone characters, cuttlebone length (unless otherwise specified) and are expressed as percentages.

Arm Length – AL : length of each designated (i.e. 1,2 etc.) arm measured from first basal (proximal-most) sucker to distal tip of arm (Arm 1, dorsal; 2, dorso-lateral; 3, ventro-lateral; 4, ventral) [ALI].	Fin Insertion anterior * – Fia : anterior origin of fin measured from mantle margin to anterior-most junction of fin and mantle [FIIa].
Anterior Mantle to Head length * – AMH : dorsal length of mantle measured from anterior-most point of mantle to intersection of transverse line joining dorso-lateral mantle margin [AMHI].	Fin Insertion posterior* – Fip : measured between posterior junctions of fins with mantle [FIIp].
Arm Sucker Count * – ASC : total number of suckers on each designated arm (e.g. ASC2).	Funnel Length – FuL : the length of the funnel from the anterior funnel opening to the posterior margin measured along the ventral midline [FuLI].
Arm Sucker diameter – AS : diameter of largest sucker on each designated (i.e. 1,2 etc.) arm [ASIn]. Suckers on left ventral hectocotyliised arms are differentiated as follows:	Fin Width – FW : greatest width of single fin [FWI].
Arm Sucker left 4 * – ASl4 : diameter of largest sucker on left ventral arm of male [ASInl4].	Gill Lamellae Count – GiLC : number of lamellae on outer demibranch including the terminal lamella.
Arm Sucker left 4 minimum * – ASl4m : diameter of smallest arm sucker on hectocotyliised portion of left ventral arm of male [ASInl4m].	Gill Length * – GiL : length of right gill [GiLI].
Cuttlebone Length – CbL : dorsal length of cuttlebone along midline, including spine (if present).	Head Length – HL : dorsal length of head measured from point of fusion of dorsal arms to anterior tip of nuchal cartilage [HLI].
Cuttlebone Width – CbW : greatest width of cuttlebone [CbWI].	Head Width – HW : greatest width of head at level of eyes [HWI].
Club Length – CIL : length of tentacular club measured from proximal-most basal suckers (carpus) to distal tip of club [CILI].	Locus Length * – LoL : length of the last locus (ventral anterior smooth zone of the cuttlebone) [LoLI].
Club Row Count – CIRC : number of suckers in transverse rows on tentacular club.	Mantle Length – ML : dorsal mantle length. Measured from anterior-most point of mantle to posterior apex of mantle.
Club Sucker diameter – CIS : diameter of largest sucker on tentacular club [CISI].	Mantle Width – MW : greatest straight-line ventral width of mantle [MWI].
Club Sucker dorsal * – CISd : diameter of largest tentacular club sucker in dorsal-most (closest to swimming keel) longitudinal row [CISId].	Spine Length * – SL : length of spine [SLI].
Club Sucker ventral * – CISv : diameter of largest tentacular club sucker in ventral-most (opposite swimming keel) longitudinal row [CISIV].	Spermatophore Length – SpL : length of spermatophore [SpLI].
Eye Diameter – ED : diameter of eye [EDI].	Spermatophore Width – SpW : greatest width of spermatophore. Spermatophore width index is expressed as a percentage of spermatophore length [SpWI].
Egg Diameter * – EgD : diameter of egg [EgDI].	Striated Zone length – StZ : length of striated zone of cuttlebone [StZI].
Free Funnel length – FFu : the length of the funnel from the anterior funnel opening to the point of its dorsal attachment to the head [FFuI].	Transverse Row Count – TrRC : number of suckers in longitudinal series on tentacular club (counted from proximal-most basal suckers (carpus) to distal tip of club).
	Ventral Mantle Length – VML : length of ventral mantle measured from anterior mantle margin at ventral midline, to posterior apex of mantle [VMLI].

Electron Optics Ltd. Japan) scanning electron microscope operated at 15 KV.

Species descriptions were generated by the DELTA (Description Language for Taxonomy) system (Dallwitz 1980; Dallwitz *et al.* 1993; Partridge *et al.* 1993).

SYSTEMATICS

Sepia plana sp. nov.

Figures 2–9; Tables 2,3 and 10

Holotype

Australia: Western Australia, North West Shelf –

M (99.3 mm ML), 14°15'S 121°59'E, 460–430 m, 25 Jan 1990, coll. RV "Courageous", (MV F77206).

Paratypes

Australia: Western Australia, North West Shelf – 1F (63 mm ML), 12°04'S 122°51'E, 420 m, 22 Jan 1990, coll. RV "Courageous", (MV F80339); 1F (100 mm ML), 12°12'S 122°48'E, 485 m, 22 Jan 1990, coll. RV "Courageous", (MV F77205); 1F (148.7 mm ML), North West Shelf, 16°54'S 120°25'E, 396 m, 12 Apr 1989, coll. FV "Striker", (MV F58848); 1F (151.2 mm ML), North West Shelf, 16°59'S 120°14'E, 405 m, 7 Apr 1989, coll. FV "Striker", (MV F77204); 2F (84.4, 127.1 mm ML), 17°55.5'S 118°16.0'E, 505 m, 2 Feb 1992, coll. FV "Surefire", (MV F67700).

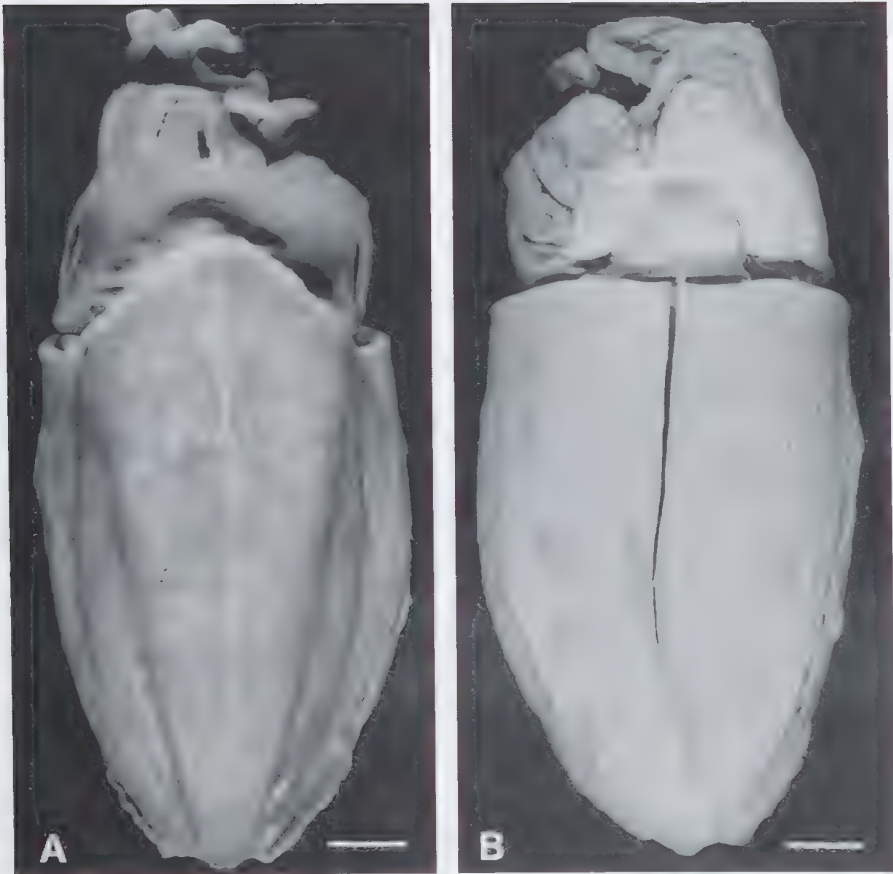


Figure 2 A–B, *Sepia plana* sp. nov.; A, dorsal view, female paratype MV F67700, 127.1 mm ML, ventral view same specimen. Scale bars 15 mm.

Additional material

Australia: Queensland – cuttlebone (broken), Lizard Island, 14°40'S 145°28'E, Nov 1989, coll. M. Norman, (MV 77203).

Diagnosis

Cuttlebone strongly angular, flat medially and laterally; dorsal surface slightly granulose; dorsal median rib indistinct; spine very short; striated zone and last loculus flat; anterior striae broad inverted U-shape; limbs of inner cone narrow, broaden only slightly posteriorly. Tentacular club with 8–10 similar-sized small suckers in transverse rows; swimming keel extends beyond carpus; dorsal and ventral protective membranes not fused at base of club, joined to stalk. Left ventral arm of males hectocotyliised: proximal 8 rows of suckers reduced, suckers in dorsal marginal series slightly smaller than remaining suckers. Arm suckers all tetraserial. Large robust species, maximum size to approximately 150 mm ML.

Description

Counts and indices for individual specimens are given in Table 2; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 3.

Large, robust species; ML male 99.3 mm, females 84.4–122.3–151.2 mm (SD, 29.5). Mantle broad, oval, MWI male 57.4, females 54.8–57.7–63.3 (SD, 3.4); dorsal anterior margin rounded (Figure 2A); extending anteriorly beyond eyes; AMHI male 16.8, females 12.2–14.8–17.3 (SD, 2.4). Ventral mantle margin slightly emarginate, without distinct lateral angle (Figure 2B); VMLI male 90.8, females 78.4–86.9–94.4 (SD, 7.3). Fins widest in posterior third; FWI male 13.8, females 7.4–9.1–10.9 (SD, 1.4); anterior origin posterior to mantle margin, set well back from margin; FIla male 14.4, females 8.9–12.7–16.4 (SD, 3.5); rounded posteriorly; wide gap between fins, FIlp male 9.3, females 9.9–11.9–14.4 (SD, 2.1). Funnel short; FuLI male 38.3, females 28.6–31.9–35.7 (SD, 3.2), robust, very broad; extends to anterior rim of eye. Funnel free portion

Table 2 *Sepia plana* sp. nov.; measurements (mm), counts and indices of 1 male (M) and 6 females (F).

Museum Reg. No.	MV F77206 (Holotype)	MV F80339 (Paratype)	MV F67700 (Paratype)	MV F77205 (Paratype)	MV F67700 (Paratype)	MV F58848 (Paratype)	MV F77204 (Paratype)
Sex	M	F	F	F	F	F	F
Maturity	mature	immature	mature	mature	mature	mature	mature
ML	99.3	63.0	84.4	100.0	127.1	148.7	151.2
MWI	57.4	61.6	63.3	57.4	55.1	57.9	54.8
AMHI	16.8	14.4	17.2	17.3	14.3	12.8	12.2
VMLI	90.8	82.2	78.4	80.6	87.6	94.4	93.6
FWI	13.8	12.2	—	10.9	7.4	8.9	9.3
FIIa	14.4	15.6	—	8.9	16.4	10.7	14.9
FIIp	9.3	10.0	—	9.9	13.0	10.5	14.4
FuLI	38.3	35.1	35.7	32.0	28.7	28.6	34.4
FFuI	16.1	14.3	14.8	13.0	11.4	17.8	15.5
HLI	26.3	40.5	—	23.2	—	27.6	—
HWI	48.8	50.8	—	46.3	48.4	44.4	39.6
EDI	12.1	17.3	—	16.1	12.4	12.4	—
ALI1	48.8	44.4	—	35.5	33.8	38.0	28.8
ALI2	40.8	41.3	—	44.5	—	44.0	36.4
ALI3	41.3	41.3	—	37.5	39.7	40.3	36.4
ALI4	45.8	41.3	—	39.5	41.3	40.0	38.4
ASIn1	1.61	1.27	—	1.07	1.08	1.26	0.89
ASIn2	1.88	1.27	—	1.12	0.98	1.31	0.99
ASIn3	1.51	1.35	—	1.00	0.90	1.21	1.04
ASIn4	1.33	1.27	—	1.00	0.79	1.26	0.96
ASC1	94	102	—	128	102	—	116
ASC2	90	110	—	136	—	—	146
ASC3	112	130	—	145	150	—	142
ASC4	118	146	—	160	172	—	145
ASInI4	1.26	—	—	—	—	—	—
ASInI4m	0.76	—	—	—	—	—	—
CILI	19.1	15.7	—	15.5	18.5	15.5	—
CIRC	8	10	—	8	—	8	—
TrRC	36	34	—	36	45	36	—
CISI	0.22	0.40	—	0.27	0.29	0.34	—
CISId	0.22	0.40	—	0.25	0.31	0.27	—
CISlv	0.22	0.32	—	0.27	0.29	0.27	—
GiLC	29	25	—	30	28	28	—
GiLI	—	34.9	31.1	37.9	42.0	37.0	—
SpLI	8.6	—	—	—	—	—	—
SpWI	4.7	—	—	—	—	—	—
EgDI	—	—	—	4.0	—	8.5	10.0
CbL	—	—	84.3	98.2	126.9	—	—
CbWI	—	—	45.4	45.8	42.9	—	—
SLI	—	—	0.6	1.4	0.4	—	—
StZI	—	—	50.9	57.0	50.7	—	—
LoLI	—	—	45.8	42.9	48.5	—	—
LoL/StZ (%)	—	—	90.0	75.2	95.6	—	—

approximately half funnel length; FFuI male 16.1, females 11.4–14.5–17.8 (SD, 2.5). Funnel organ dorsal elements thick, inverted V-shape; ventral elements oval (Figure 3A). Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression which corresponds to ridge (Figure 3B). Head short; HLI male 26.3, females 23.2–25.4–27.6 (SD, 3.1); broad, narrower than mantle; HWI male 48.8, females 39.6–44.7–48.4 (SD, 3.7). Eyes large; EDI male 12.1, females 12.4–13.7–16.1 (SD, 2.1); ventral eyelids present (Figure 2A).

Male and female arms subequal in length (Table 3). Arm length index of longest arms in male 48.8, females 36.4–41.6–44.5 (SD, 4.6). Protective membranes (both sexes) narrow; normal, not thickened. Distal arm tips (both sexes) strongly attenuate, suckers enclosed by protective membranes. Arm suckers tetraserial in both sexes. Suckers in males normal in size (not greatly enlarged); larger than female arm suckers (Table 3). Inner ring of chitinous sucker rims with blunt projections; infundibulum with 12–14 rows of ovoid-hexagonal processes without pegs,

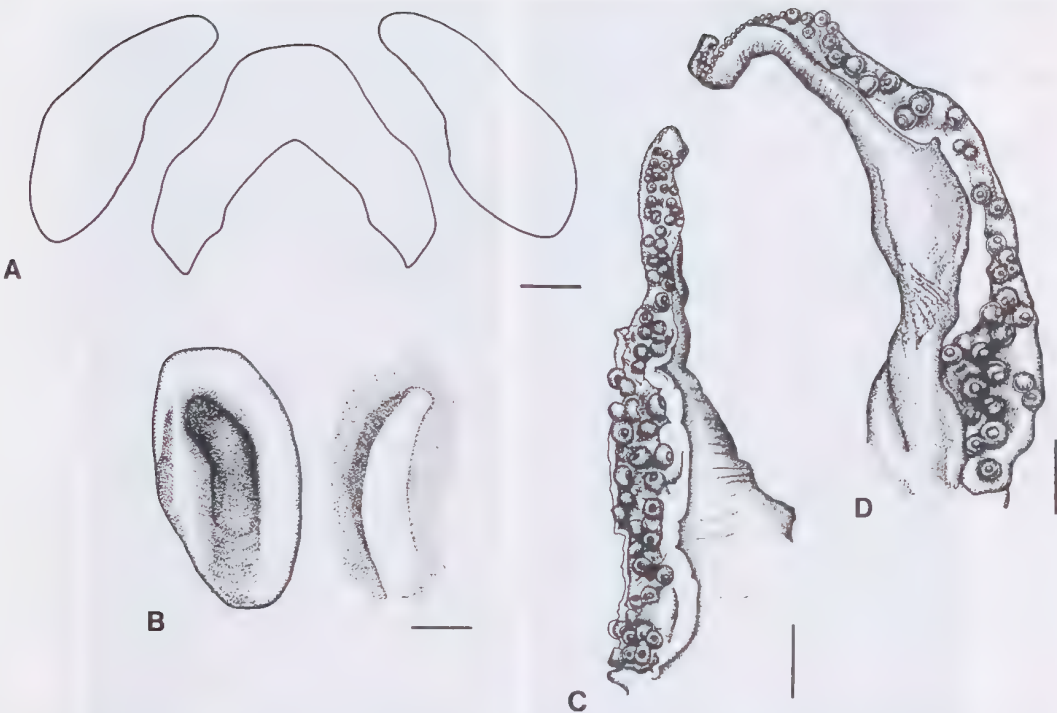


Figure 3 A–D, *Sepia plana* sp. nov.; A, funnel organ, scale bar 3 mm; B, funnel-locking cartilage (left), and mantle-locking cartilage (right), scale bar 1 mm; C, hectocotylied left ventral arm, scale bar 3 mm; D, right ventral arm, scale bar 3 mm. (A–D male holotype MV F77206, 99.3 mm ML).

innermost row large, rectangular-hexagonal; peripheral sucker rim processes radially arranged, slightly more elongate (Figure 4A). Sucker counts range from 90–172; females with higher average counts than male (Table 3).

Table 3 *Sepia plana* sp. nov.; arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 1 mature male and ranges of these measures and counts for 5 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Male	Females			
		min.	mean	max.	SD
ALI1	48.8	28.8	<u>34.0</u>	38.0	3.9
ALI2	40.8	36.4	<u>41.6</u>	44.5	4.6
ALI3	41.3	36.4	<u>38.5</u>	40.3	1.9
ALI4	45.8	38.4	<u>39.8</u>	41.3	1.2
ASIn1	1.61	0.89	<u>1.07</u>	1.26	0.15
ASIn2	1.88	0.98	<u>1.10</u>	1.31	0.15
ASIn3	1.51	0.90	<u>1.04</u>	1.21	0.13
ASIn4	1.33	0.79	<u>1.00</u>	1.26	0.19
ASC1	94	102	<u>115</u>	128	13
ASC2	90	136	<u>141</u>	146	7
ASC3	112	142	<u>146</u>	150	4
ASC4	118	145	<u>159</u>	172	14

Left ventral arm of male hectocotylied: suckers slightly reduced in size (Figure 3C,D), maximum and minimum sucker diameters: ASInl4 1.26, ASInl4m 0.76 (compare with non-hectocotylied arms Table 3); proximal 8 rows (approximately) of suckers reduced; suckers in dorsal marginal series slightly smaller than remaining suckers. Oral surface of modified region wide, fleshy, with transversely grooved ridges; without distinct median furrow. Hectocotylied arm not markedly attenuate distally.

Tentacular club longer in male than in females; CLI1 male 19.1, females 15.5–16.5–18.5 (SD, 1.7). Club crescent-shaped; sucker-bearing face flattened. Club with 8–10 suckers in transverse rows, CIRC male 8, females 8–9–10 (SD, 1); 36–45 suckers in longitudinal series, TrRC male 36, females 36–39–45 (SD, 5). Suckers all similar size, small (Figure 5A), CISI male 0.22, females 0.27–0.30–0.34 (SD, 0.03); dorsal and ventral-marginal longitudinal series of suckers similar size; CISId males 0.22, females 0.25–0.28–0.31 (SD, 0.03); CISIv male 0.22, females 0.27–0.28–0.29 (SD, 0.01). Sucker dentition: inner ring with blunt projections; infundibulum with 8–9 rows of ovate polygonal processes without pegs; innermost row processes

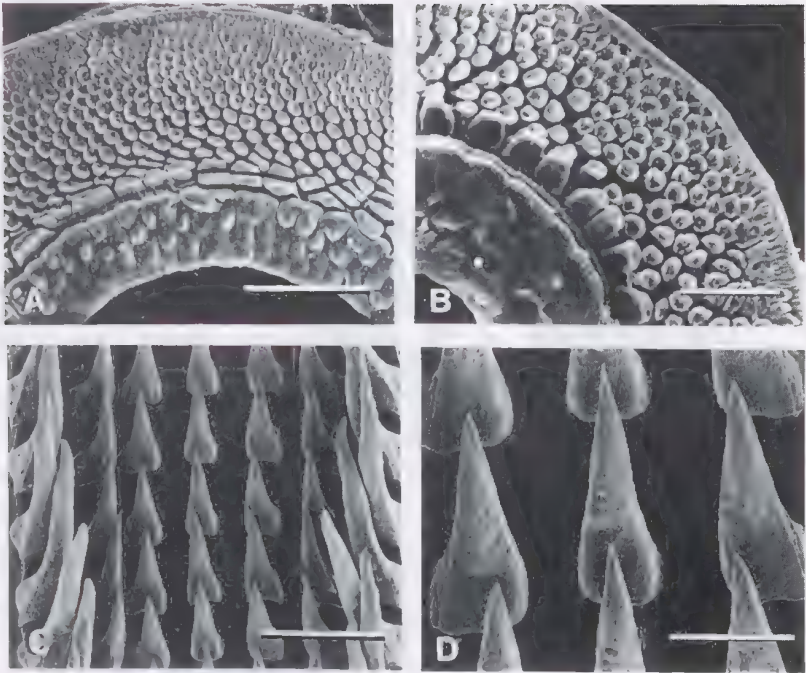


Figure 4 A–D, *Sepia plana* sp. nov.; A, arm 2 sucker rim, female paratype MV F77205, 100 mm ML, scale bar 100 μ m; B, club sucker rim, female paratype MV F67700, 127.1 mm ML, scale bar 40 μ m; C, radula, female paratype MV F77205, 100.0 mm ML, scale bar 500 μ m; D, enlargement of 1st laterals and rhachidian (centre) teeth, same specimen, scale bar 200 μ m.

elongate, rectangular; at periphery processes smaller, sub-rectangular (Figure 4B). Swimming keel of club extends well beyond carpus (Figure 5A). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal and ventral membranes same length, extend beyond carpus along stalk; approximately equal width; dorsal membrane forms shallow cleft at junction with stalk.

Gills with 28–30 lamellae per demibranch; GiLC male 29, females 28–29–30 (SD, 1). Gill length: GiLI females 31.1–37.0–42.0 (SD, 4.5).

Buccal membrane without suckers. Upper beak (Figure 5B) rostrum bluntly pointed, length greater than width; cutting edge slightly curved; hood high above crest posteriorly; lateral wall shallowly indented posteriorly; wings and hood narrow, and short; jaw angle approximately 90°; hood dark brown, lighter on posterior edge, crest darkly pigmented. Lower beak (Figure 5C,D) rostrum bluntly pointed, protrudes only slightly; cutting edge curved; hood low on crest; crest straight, no indentation on lateral wall edge; hood and wings, width narrow; hood notch deep, broad (Figure 5D); wings widely spaced; crest wide with deep notch; rostrum pigmented dark brown, fading gradually on wing, crest pigmented, darkest medially fades on lateral walls. Radula with 7 teeth per row;

homodont; rhachidian teeth narrow, not broad based, slender, triangular, sides straight (Figure 4C,D); first lateral teeth same length as rhachidian teeth, asymmetrical with mesocone displaced toward centre of radula, heel narrow (Figure 4C,D); second laterals longer than first, mesocone displaced towards centre, heel broad; marginal teeth elongate, tapered, curved, rounded proximally and strongly indented (Figure 4C). Digestive tract (Figure 5E): paired salivary glands approximately one-third length of buccal mass; paired digestive glands large, located close together, with sub-triangular lobes posteriorly, ducts connect digestive glands near midline with caecum (not shown in figure), ducts with branched attached pancreatic tissue; oesophagus runs dorsally along median junction of digestive glands, joins sac-like stomach immediately posterior to digestive glands; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens opens into broad cone-shaped mucilaginous gland, then narrower, curved spermatophoric gland (Figure 6A). Close to junction with lobe-shaped accessory gland and

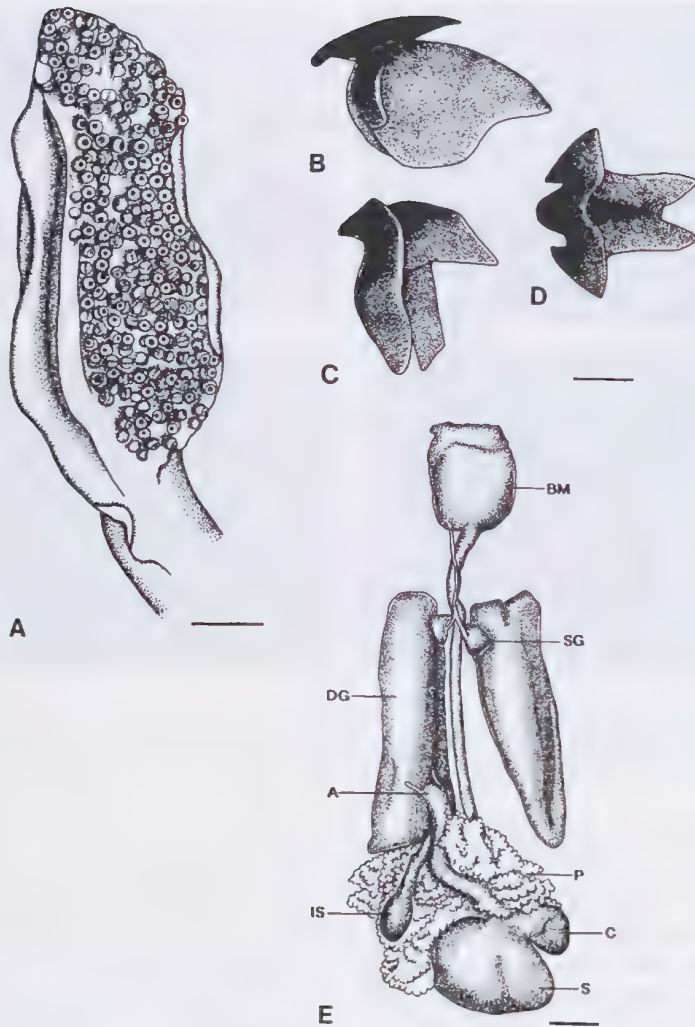


Figure 5 A–E, *Sepia plana* sp. nov.; A, tentacular club, female paratype MV F77205, 100.0 mm ML, scale bar 2 mm; B, upper beak, lateral view; C, lower beak, lateral view; D, lower beak, ventral view (B–D, male holotype MV F77206, 99.3 mm ML, scale bar 3 mm); E, digestive tract, female paratype (MV F80339), 63.0 mm ML, scale bar 6 mm, (A – anus; BM – buccal mass; C – caecum; DG – digestive gland; IS – ink sac; P – pancreas; S – stomach; SG – salivary gland).

gland appendix, delicate ciliated canal joins spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophore storage sac; genital orifice opens dorsal to left gill in anterior end of mantle cavity. Spermatophores: cement body bipartite (Figures 6B, 7); aboral end elongate, cylindrical, connects to sperm reservoir via narrow duct which extends from tip of cement body; oral end of cement body approximately half length of aboral end, similar width; connects to aboral end via narrow neck; middle tunic commences along aboral part of cement body; ejaculatory apparatus coiled, extends

into oral dilation of spermatophore. Spermatophores 8.5 mm long, 0.4 mm wide; SpLI 8.6; SpWI 4.7.

Female reproductive tract: ovary hangs from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands in mature animals occupy large portion of ventral side of mantle cavity. Accessory nidamental glands anterior to nidamental glands (Figure 6C). Eggs spherical, 4.0–7.5–10.0 mm diameter (SD, 3.1); EgDI 4.0–5.4–6.6 (SD, 1.3).

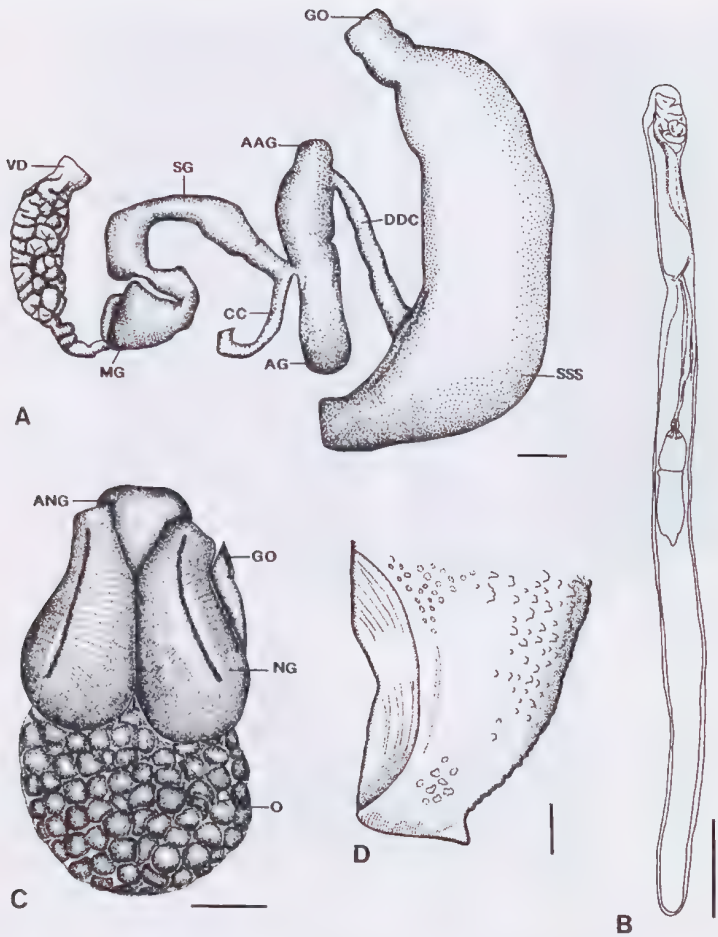


Figure 6 A–D, *Sepia plana* sp. nov.; A, male reproductive tract (testis not shown), holotype MV F77206, 99.3 mm ML, scale bar 1 mm, (AAG – appendix of accessory gland; AG – accessory gland; CC – ciliated canal; DDC – distal deferent canal; GO – genital orifice; MG – mucilaginous gland; SG – spermatophoric gland; SSS – spermatophore storage sac; VD – vas deferens); B, spermatophore, holotype MV F77206, 99.3 mm ML, scale bar 1 mm; C, female reproductive tract, paratype MV F77205, 100 mm ML, scale bar 20 mm, (ANG – accessory nidamental gland; GO – genital orifice; NG – nidamental gland; O – ovary); D, posterior end of cuttlebone, lateral view, female paratype MV F67700, 84.4 mm ML, scale bar 1 mm.

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oval (Figure 8A,B); CbL females 84.3–103.1–126.9 (SD, 21.7); CbWI females 42.9–44.7–45.8 (SD, 1.6). Cuttlebone bluntly rounded anteriorly; acuminate, acute posteriorly (Figure 8A,B); recurved ventrally (Figure 6D). Dorsal surface creamy white; flat medially, flat laterally (Figure 8A); granulose (Figure 8C). Dorsal median rib present, indistinct, broadens anteriorly; lateral ribs present, distinct. Chitin borders lateral margins of cuttlebone. Spine present, short (Figures 6D, 8A,C); SLI females 0.4–0.8–1.4 (SD, 0.5); curves dorsally (Figure 6D);

keel(s) absent; cuttlebone smooth between spine and outer cone; ventral notch at base of spine absent. Dorso-posterior end of cuttlebone smooth, without median longitudinal ridge anterior to spine. Striated zone flat; StZI females 50.7–52.9–57 (SD, 3.6). Last loculus flat; LoLI females 42.9–45.7–48.5 (SD, 2.8); slightly shorter than striated zone, LoL/StZ(%) females 75.2–86.9–95.6 (SD, 10.6). Sulcus absent. Anterior striae broad inverted U-shape (Figure 8B). Limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs narrow, broaden very slightly posteriorly, not raised to form ledge posteriorly; not thickened posteriorly. Outer cone calcified; narrow

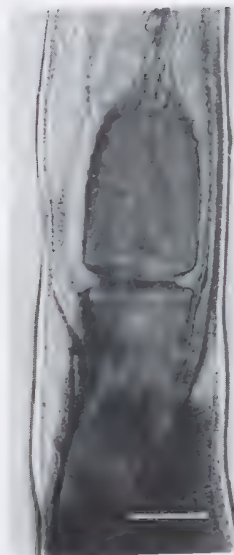


Figure 7 *Sepia plana* sp. nov.; middle portion of ejaculatory apparatus of spermatophore, holotype MV F77206, 99.3 mm ML, scale bar 100 μ m.

anteriorly, broadens posteriorly (Figure 8B); lateral limbs not flared ventro-laterally; limbs continue as broad ledge ventral to spine (Figure 6D).

Body papillae present. Ventral mantle with longitudinal row of up to 5 narrow ridges along each side, close to fins (not visible in all specimens). Head and arm papillae absent. Colour (alcohol preserved specimens): head and arms pale buff pinkish-brown; dorsal mantle pale buff pinkish-brown; paired dorsal eye spots absent. Fins pale; without markings at base. Ventral pigment absent. Ventral longitudinal ridges pale orange.

Type locality

Australia: Western Australia, North West Shelf, 14°15'S 121°59'E; 460–430 m.

TYPE: Holotype, MV F77206, male, 99.3 mm ML.

Distribution

Australia: Western Australia, North West Shelf, 12°04'S 122°51'E – 17°55.5'S 118°16.0'E (Figure 9); depth range 505–396 m. May also occur off eastern Australia (see Remarks).

Etymology

The specific name, *plana*, is derived from the Latin *planus* meaning “level” or “flat”, and refers to the flattened dorsal and lateral sides of the cuttlebone in this species. Gender feminine.

Remarks

A single sepiion was collected on Lizard Is., off

Queensland, 14°40'S 145°28'E in November 1989. This suggests that this species may also occur off the northeastern Australian coast, though the possibility that the sepiion was carried by currents from the west cannot be excluded. The elongate appearance of the innermost row of polygonal processes on the club sucker ring infundibulum (Figure 4B) may be due to contraction of the suckers during drying for SEM preparation. The dorsal funnel organ element seems to lack an anterior papilla in this species. However, the funnel organs were damaged in most specimens. The absence of the anterior papilla needs to be confirmed when additional well-preserved material becomes available.

Determination of the relationships of *Sepia plana* sp. nov. to other species is at present difficult owing to the general confusion of relationships within *Sepia*, and the lack of comprehensive descriptions for many of the nominal species within the genus. While some species ‘complexes’ have been recognised (e.g. Khromov *et al.*, in press; Lu, in press b), these may not be monophyletic. These complexes are not tightly defined, based on few characters, and differ among authors, so assignment of *S. plana* sp. nov., or the other species described in this paper, to a particular complex is of limited value. For these reasons, it is difficult to select those species from among the 100 or so nominal sepiids which are of particular interest for comparison of individual characters with *S. plana* sp. nov. Some characters are shared between *S. plana* sp. nov. and other species, while other characters differ. The structure of the cuttlebone, however, with its distinctive flattened dorsal and lateral margins distinguishes *S. plana* sp. nov. from all other nominal species in the genus.

Sepia senta sp. nov.

Figures 9–16; Tables 4–6 and 10

Holotype

Australia: Western Australia, North West Shelf – M (41.5 mm ML), 14°07'S 122°06'E, 415 m, 25 Jan 1990, coll. V. Wadley on RV “Courageous”, (MV F77200).

Paratypes

Australia: Western Australia, North West Shelf – 1F (64.2 mm ML), 13°45'S 122° 39'E, 420 m, 23 Jan 1990, coll. RV “Courageous”, (MV F77195); 7M (42.1–61.6 mm ML) 2F (54.6, 54.7 mm ML), NW of Cape Leveque, 14°50.2'S 121°31.4'E – 14°48.6'S 121°33.2'E, 356 m, 12 Feb 1984, coll. S. Slack-Smith on RV “Soela”, (WAM 332–86); 3F (62.5–83.2 mm ML), NW of Cape Leveque, 14°51.9'S 121°40.6'E – 14°54.0'S 121°39.1'E, 260–256 m, 16 Feb 1984, coll. S. Slack-Smith on RV “Soela”, (WAM 104–96); 1M

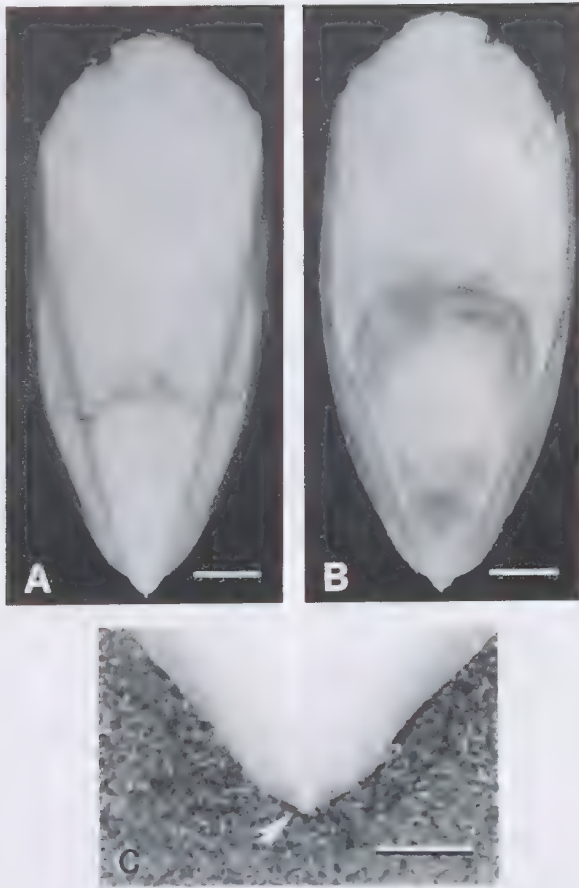


Figure 8 A–C, *Sepia plana* sp. nov.; A, cuttlebone, dorsal view, female paratype MV F77205, 100.0 mm ML, scale bar 10 mm; B, cuttlebone, ventral view, same specimen, scale bar 10 mm; C, posterior end of cuttlebone, dorsal view, female paratype MV F67700, 127.1 mm ML, arrow indicates spine, scale bar 1.5 mm.

(49.8 mm ML) 1F (48.2 mm ML), North West Shelf 18°06'S 118°6'E, 340 m, 28 Feb 1983, coll. RV "Soela", (MV F77197); 1F (43.4 mm ML), North West Shelf, 18°25'S 117°48'E, 375 m, 2 Aug 1988, coll. RV "Soela", (MV F77199).

Additional Material

Australia: Western Australia, North West Shelf – 1F (65.0 mm ML), 12°04'S 122°51'E, 420 m, 22 Jan 1990, coll. RV "Courageous", (MV F80340); 1M 1J (62.0, 16.6 mm ML), NW of Augusta, 14°29.4'S 122°01.4'E – 14°28.4'S 122°03.2'E, 304–296 m, 12 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 334–86); 2M (56.5, 65.0 mm ML) 2F (68.2, 74.5 mm ML), NNW of Cape Leveque, 14°35.8'S 121°49.4'E – 14°37.2'S 121°47.4'E, 304–300 m, 16 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 103–96); 2M (56.2, 61.5 mm ML) 11F (52.9–77.2 mm ML), NW of Cape Leveque, 14°49.0'S 121°36.1'E – 14°50.8'S 121°35.6'E, 302–300 m, 12 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 264–88); 1M (67.5 mm

ML), NW of Cape Leveque, 15°11.1'S 12°26.9'E – 15°12.9'S 121°25.7'E, 260–258 m, 17 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 102–96); 1M (36.5 mm ML) 2F (32.0, 37.3 mm ML), NW of Beagle Bay, 15°13.5'S 121°08.9'E – 15°15.0'S 121°06.5'E, 352 m, 11 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 331–86); 1M (61.9 mm ML) 2F (55.7, 57.1 mm ML), WNW of Lacepede Archipelago, 15°48.0'S 120°41.0'E – 15°50.1'S 120°39.5'E, 400–396 m, 10 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 329–86); 1M (58.7 mm ML), W of Lacepede Archipelago, 16°55.8'S 119°53.9'E – 17°01.8'S 119°51.3'E, 426 m, 19 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 263–88); 1F (75.3 mm ML), North West Shelf, 16°58'S 120°13'E, 413 m, 2 Apr 1989, coll. S. Morris on FV "Striker", (MV F77201); 1F (48.9 mm ML), W of Broome, 17°59'S 118°23'E – 17°54'S 118°29'E, 390–389 m, 24 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 349–86); 1F (31.0 mm ML), W of Roebuck Bay, 18°04'S 118°14'E – 18°00'S 118°19'E,

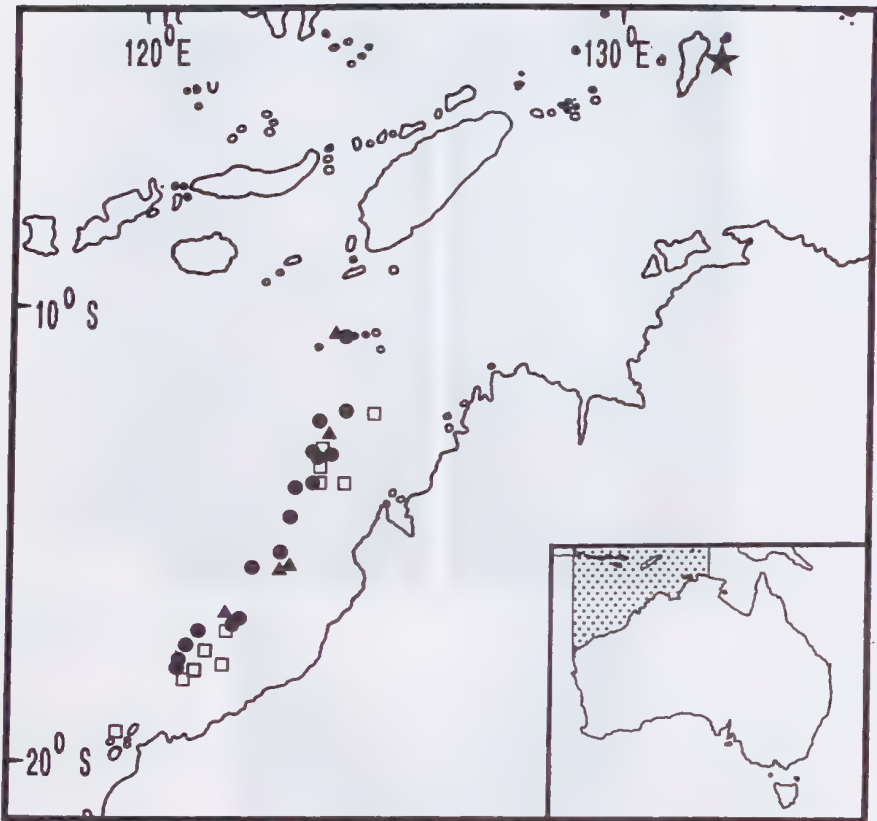


Figure 9 Distributions of *Sepia plana* sp. nov. (triangles), *S. senta* sp. nov. (solid circles), and *S. sulcata* Hoyle (open squares). The type locality of *S. sulcata* is indicated by a star (top right of figure).

400–396 m, 24 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 346–86); 1F (60.7 mm ML), North West Shelf, 18°33'S 117°36'E – 18°33'S 117°38'E, 356–344 m, 17 Aug 1983, coll. RV "Soela", (MV F77198); 1F (58.6 mm ML), North West Shelf, 18°35'S 117°29'E, 404 m, 31 Jan 1984, coll. P. Berry & N. Sinclair on RV "Soela", (MV F77196); 1F (67.3 mm ML), N of Karratha, 18°44'S 116°59'E, 406–404 m, 23 Aug 1983, RV "Courageous", (WAM 4292–83).

Diagnosis

Cuttlebone oval; dorsally rough, with irregular calcified projections; thin chitinous film covers entire dorsal surface; spine absent; sulcus absent, anterior striae slightly convex to straight. Club with 6–8 suckers in transverse rows; suckers small, differ slightly in size; dorsal and ventral protective membranes not fused at base of club; joined to stalk; differ in length, ventral protective membrane terminates at posterior end of carpus, dorsal membrane shorter than carpus; swimming keel extends slightly beyond carpus. Left ventral arm

hectocotylied in males: proximally a single row of normal suckers, followed distally by 8–11 rows of greatly reduced suckers, 2 dorsal series smaller than 2 ventral series; oral surface wide, fleshy; remaining suckers normal. Small to moderate species, maximum size to approximately 80 mm ML. Arm lengths subequal, suckers tetraserial on all arms.

Description

Counts and indices for individual specimens are given in Tables 4–5; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 6.

Small to moderate species, ML males 41.5–53.9–61.6 83.2 mm (SD, 6.5), females 43.4–61.6–75.3 83.2 mm (SD, 9.8). Mantle broad, oval (Figure 10A,B); MWI males 49.3–60.4–69.2 (SD, 7.5), females 55.5–62.6–69.9 (SD, 4.9); dorsal anterior margin triangular, obtuse; extending to anterior margin of eyes; AMHI males 14.3–18.9–25.1 (SD, 3.5), females 14.4–20.7–26.8 (SD, 4.6). Ventral mantle margin emarginate, without distinct lateral angle; VMLI

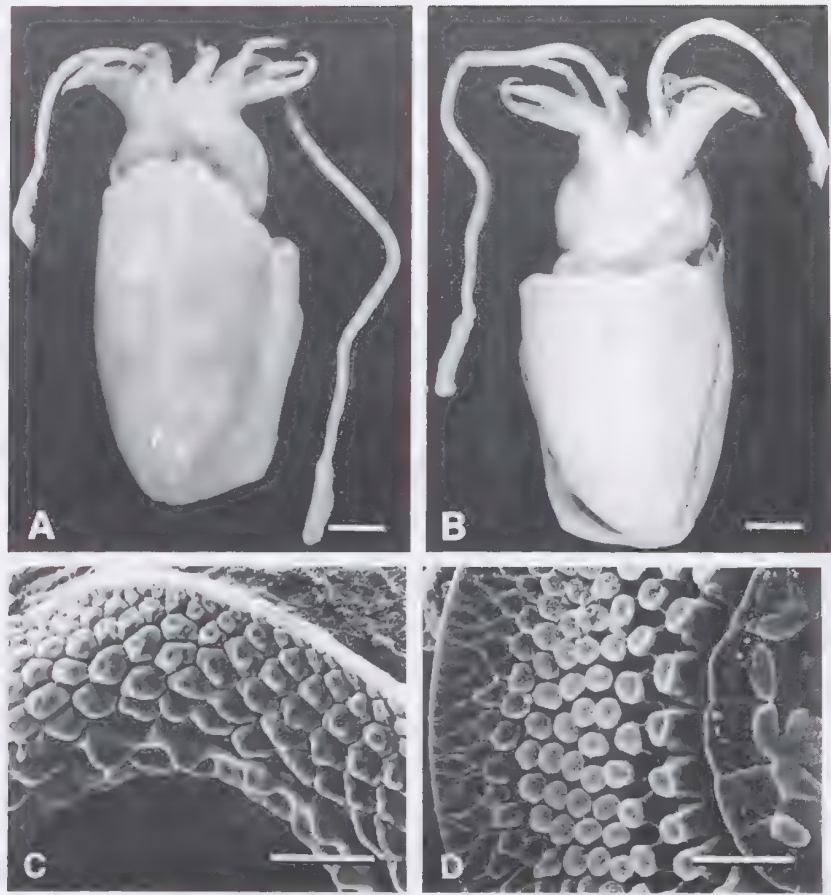


Figure 10 A–D, *Sepia senta* sp. nov.; A, dorsal view, female paratype MV F77195, 64.2 mm ML, scale bar 10 mm; B, ventral view same specimen, scale bar 10 mm; C, sucker rim, hectocotyliized arm 4, male paratype MV F77197, 49.8 mm ML, scale bar 30 µm; D, club sucker rim, female paratype MV F77197, 48.2 mm ML, scale bar 10 mm.

males 77.9–87.0–92.6 (SD, 5.1), females 68.1–81.1–89.8 (SD, 7.3). Fins widest in posterior third; FWI males 6.5–9.7–12.0 (SD, 2.1), females 9.7–12.5–16.2 (SD, 2.4); anterior origin posterior to mantle margin (Figure 10A,B); FIIa males 10.4–12.8–15.1 (SD, 1.8), females 11.4–14.3–19.3 (SD, 2.4); rounded posteriorly; narrow gap between fins; FIIP males 5.8–8.2–10.2 (SD, 1.5), females 3.5–8.6–11.9 (SD, 3.0). Funnel long, FuLI males 28.0–34.8–39.1 (SD, 3.5), females 30.0–35.0–39.6 (SD, 2.9); broad-based; extends to anterior rim of eye. Funnel free portion approximately one-third funnel length (slightly greater in females); FFuI males 9.6–12.9–16.9 (SD, 2.3), females 11.3–14.8–18.7 (SD, 2.5). Funnel organ dorsal elements inverted V-shape with small papilla in front; ventral elements oval (Figure 11A). Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with depression which corresponds to ridge (Figure 11B). Head

short (Figure 10A,B), HLI males 23.7–33.8–44.6 (SD, 6.3), females 21.9–31.4–35.2 (SD, 3.8); broad, narrower than mantle, HWI males 41.2–47.9–54.5 (SD, 4.3), females 43.8–47.8–51.3 (SD, 2.8). Eyes large, EDI males 11.9–13.9–16.6 (SD, 1.5), females 10.8–12.6–15.0 (SD, 1.6); ventral eyelids present.

Male and female arms subequal in length (Table 6); ALI of longest arms in males 39.8–47.8–61.4 (SD, 5.9), females 36.9–45.3–54.9 (SD, 5.0). Protective membranes (both sexes) narrow; normal, not thickened. Distal arm tips (both sexes) not markedly attenuate. Arm suckers tetraserial in both sexes. Suckers in males normal in size (not greatly enlarged), larger than female arm suckers (Table 6). Chitinous rims of all arm suckers with smooth, or only slightly crenulated inner ring; infundibulum with 7–11 rows of hexagonal processes with blunt pegs (Figure 10C); peripheral sucker rim processes radially arranged, elongate,

Table 4 *Sepia sentia* sp. nov.; measurements (mm), counts and indices of 10 mature males from Australia, and a single mature male (species not determined) from the Philippines (see remarks).

Museum Reg. No.	MV F77200 (Holotype)	WAM 332-86 (Paratype)	MV F77197 (Paratype)	WAM 332-86 (Paratype)	WAM 332-86 (Paratype)	WAM 264-88	WAM 332-86 (Paratype)	WAM 263-88	WAM 264-88	MV 332-86 (Paratype)	MV F77982 (Philippines)
ML	41.5	47.3	49.8	51.5	54.0	56.2	57.3	58.7	61.5	61.6	45.4
MW1	69.2	62.4	66.3	49.3	57.6	67.8	49.7	68.5	57.9	55.2	59.5
AMH1	22.2	14.8	25.1	22.3	16.6	18.9	16.7	18.9	14.3	19.5	17.2
VML1	79.8	92.6	77.9	82.5	91.3	89.3	90.2	88.9	89.8	87.5	83.5
FW1	12.0	10.8	-	10.1	6.5	-	8.9	8.0	-	11.9	9.0
Fla	14.7	14.6	12.0	14.6	10.4	11.9	10.5	11.9	12.5	15.1	16.5
Flp	8.4	8.9	10.2	7.2	7.0	9.6	9.4	-	7.0	5.8	11.7
FuL1	28.0	35.9	31.9	37.9	34.4	39.1	34.0	35.8	39.0	32.1	37.2
FFul	16.9	13.7	12.0	14.6	14.8	11.6	9.6	10.2	11.4	14.6	15.4
HL1	44.6	38.3	36.1	35.3	30.4	38.6	32.3	23.7	33.5	25.0	31.7
HW1	54.5	51.0	50.6	47.6	47.4	45.9	41.2	52.6	46.7	41.9	55.5
EDI	16.6	14.2	14.5	13.2	13.9	13.3	12.9	16.2	11.9	12.3	13.7
AL11	50.6	49.7	43.2	42.7	50.9	49.8	50.6	39.2	41.5	42.2	34.1
AL12	54.2	46.5	39.2	40.8	51.9	42.7	51.5	42.6	39.0	42.2	33.0
AL13	61.4	48.6	45.2	46.6	50.9	49.8	48.9	44.3	42.3	39.8	33.0
AL14	51.8	48.6	53.2	41.7	39.8	55.2	42.8	42.6	48.0	43.0	43.0
ASin1	2.41	2.64	2.51	2.68	2.76	2.67	2.62	2.33	2.31	2.44	1.65
ASin2	2.41	2.64	2.51	2.62	2.87	2.33	2.18	2.33	2.18	2.44	1.65
ASin3	2.89	2.43	2.51	2.62	2.41	2.58	2.27	2.04	2.44	2.44	1.65
ASin4	2.41	2.11	2.15	2.45	2.19	2.22	2.18	1.91	2.44	2.03	1.59
ASC1	74	84	68	78	75	78	62	64	68	80	72
ASC2	78	76	64	85	96	80	82	82	66	78	84
ASC3	80	98	89	94	109	96	82	82	70	107	96
ASC4	116	134	120	140	119	144	164	120	140	138	114
ASin14	0.95	0.95	1.10	0.76	1.19	0.89	1.05	-	0.81	0.73	1.32
ASin14m	0.60	0.85	0.74	0.58	0.74	0.48	0.87	-	0.36	0.49	-
CIL1	33.7	27.5	30.1	30.1	29.6	33.8	24.4	20.4	26.0	24.4	22.0
CIRC	7	8	7	8	6	7	7	7	7	8	9
TrRC	25	28	31	25	30	32	24	22	28	26	33
CIS1	0.84	1.27	1.00	1.17	0.89	1.01	1.08	0.77	1.06	0.97	0.37
CIS1d	0.89	0.85	0.70	1.05	0.81	0.80	0.87	0.72	0.93	0.88	0.26
CIS1v	0.65	0.76	0.50	0.58	0.81	0.75	0.65	0.72	0.60	0.63	0.33
GiLC	20	22	22	20	22	-	22	-	-	22	25
GiLi	28.2	41.2	33.5	29.7	25.7	38.8	21.8	39.0	36.1	30.7	33.0
SpL1	13.3	11.2	12.0	9.3	10.2	11.6	9.2	10.2	8.9	9.7	-
SpWI	2.73	3.79	3.33	4.17	3.64	3.85	3.77	3.33	3.64	3.67	-
CbL	-	47.0	50.1	50.5	53.3	54.2	55.3	57.6	59.4	58.3	42.1
CbWI	-	49.1	48.9	45.7	48.6	46.1	44.5	44.5	42.4	44.1	55.1
StZ1	-	56.2	55.5	55.6	56.3	58.5	60.6	50.3	55.9	59.5	54.4
LoL1	-	41.1	42.1	43.8	42.1	36.2	39.2	40.8	37.9	40.3	33.7
LoL/StZ(%)	-	73.1	75.9	78.6	71.7	61.8	64.8	81.0	67.8	67.7	62.0

Table 5 *Sepia senta* sp. nov.; measurements (mm), counts and indices of 10 mature females.

Museum Reg. No.	MV F77199 (Paratype)	MV F77197 (Paratype)	MV F77196	MV F77198	WAM 264–88	MV F77195 (Paratype)	WAM 264–88	WAM 264–88	WAM 264–88	MV F77201
ML	43.4	48.2	58.6	60.7	60.9	64.2	65.6	67.8	71	75.3
MWI	57.6	69.9	58.4	60.8	67.3	55.5	65.5	65.9	59.0	65.7
AMHI	25.1	26.8	25.1	22.7	16.4	22.4	15.7	16.1	14.4	22.6
VMLI	82.9	72.0	79.2	78.9	86.2	77.1	89.8	87.8	88.7	68.1
FWI	9.7	–	14.7	13.2	11.5	11.5	15.2	16.2	9.7	10.8
FIla	15.0	11.4	11.4	14.7	13.5	16.0	13.1	19.3	14.1	–
FIIp	3.5	7.5	7.7	5.9	7.4	–	11.9	11.9	11.8	9.8
FuLI	37.6	36.3	30.0	33.8	36.1	34.3	39.6	37.3	33.8	31.3
FFuI	18.4	18.7	14.5	12.4	14.8	15.6	16.8	13.3	12.7	11.3
HLI	31.3	33.0	–	32.5	32.0	31.2	32.2	33.3	35.2	21.9
HWI	43.8	49.6	47.6	45.0	50.6	43.9	50.0	48.8	47.2	51.3
EDI	14.7	10.8	15.0	13.3	10.8	11.7	11.3	12.5	14.1	12.1
ALI1	35.7	40.5	45.2	44.5	37.8	34.3	43.4	44.2	42.3	38.5
ALI2	38.0	39.4	46.1	49.4	40.2	45.2	51.1	47.2	48.6	39.8
ALI3	36.9	41.5	45.2	47.8	44.3	42.8	54.9	47.2	50.0	42.5
ALI4	39.2	45.6	39.2	46.1	46.8	45.2	48.8	47.9	46.5	47.8
ASIn1	1.73	1.80	2.00	2.06	1.74	1.71	1.83	1.55	1.79	1.79
ASIn2	2.00	1.87	1.91	2.06	2.15	1.56	1.75	1.58	1.76	1.79
ASIn3	1.61	1.66	2.13	2.01	1.84	1.79	1.60	1.65	1.58	1.42
ASIn4	1.84	1.80	1.91	1.68	1.76	1.71	1.71	1.84	1.41	1.33
ASC1	80	88	102	96	100	107	92	90	86	100
ASC2	98	112	100	115	90	116	112	116	116	114
ASC3	114	120	118	130	118	132	120	130	130	128
ASC4	122	140	128	140	136	150	156	150	153	140
CILI	–	28.0	34.1	32.1	34.5	28.0	34.3	28.0	26.8	31.9
CIRC	–	7	7	7	7	7	7	7	7	7
TrRC	–	27	37	26	27	32	29	24	25	32
CISI	–	1.04	1.23	1.15	1.10	1.28	0.99	0.96	0.70	1.00
CISId	–	0.73	0.80	0.66	0.94	0.78	0.69	0.91	0.63	0.66
CISlv	–	0.52	0.55	0.61	0.82	0.58	0.69	0.69	0.49	0.66
GiLC	23	–	23	25	–	25	23	–	–	–
GiLI	33.6	40.7	26.1	34.1	37.9	31.5	40.9	33.5	34.1	36.5
EgDI	–	–	–	–	–	–	5.5	8.3	5.9	6.6
CbL	43.3	47.6	55.4	59.7	62.0	63.2	63.7	67.1	69.4	75.4
CbWI	50.8	46.4	48.7	45.7	50.2	47.9	46.3	43.2	43.1	43.0
StZI	54.5	52.7	–	52.6	47.9	51.4	45.5	47.7	55.9	52.1
LoLI	42.7	47.7	47.3	46.9	49.2	50.8	46.8	45.0	40.5	48.4
LoL/StZ (%)	78.4	90.4	–	89.2	102.7	98.8	102.8	94.4	72.4	92.9

with or without pegs. Sucker counts range from 62–164; females with higher average counts than males (Table 6).

Left ventral arm of male hectocotylied: sucker size normal proximally, reduced distally, then normal to arm tip (Figure 11C, compare with Figure 11D); from proximal to distal end of arm, 1 row of normal suckers (slightly larger than rest), 8–11 rows of reduced suckers; suckers in 2 dorsal series smaller than rest in series (dorsal-marginal series slightly larger than dorso-medial series); reduction marked, maximum and minimum sucker diameters hectocotylied arm, ASIn14 0.73–0.93–1.19 (SD, 0.16), ASIn14m 0.36–0.63–0.87 (SD, 0.18) (compare with non-hectocotylied arms Table 6); 2 dorsal and 2 ventral series of suckers widely spaced. Oral surface wide, fleshy, with transversely grooved ridges (Figure 11C); without distinct

median furrow. Right ventral arm slightly thickened, fleshy, with slightly reduced suckers. Hectocotylied arm not markedly attenuate distally.

Tentacular club similar length in males and females; CILI males 20.4–28.0–33.8 (SD, 4.3), females 26.8–30.9–34.5 (SD, 3.1). Club crescent-shaped; sucker-bearing face flattened. Club with 6–8 suckers in transverse rows, CIRC males 6–8–8 (SD, 1), females 7; 22–37 suckers in longitudinal series, TrRC males 22–27–32 (SD, 3), females 24–29–37 (SD, 4.2). Suckers small differ slightly in size; (Figure 12A); CISI males 0.77–1.01–1.27 (SD, 0.15), females 0.70–1.05–1.28 (SD, 0.17); dorsal-marginal series of suckers slightly larger than those in ventral-marginal series row; CISId males 0.70–0.85–1.05 (SD, 0.10), females 0.63–0.76–0.94 (SD, 0.11); CISlv males 0.50–0.67–0.81 (SD, 0.09), females

Table 6 *Sepia senta* sp. nov.; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males					Females			
	min.	mean	max.	SD		min.	mean	max.	SD
ALI1	39.2	<u>46.0</u>	50.9	4.7		34.3	<u>40.6</u>	45.2	3.9
ALI2	39.0	<u>45.1</u>	54.2	5.6		38.0	<u>44.5</u>	51.1	4.7
ALI3	39.8	<u>47.8</u>	61.4	5.9		36.9	<u>45.3</u>	54.9	5.0
ALI4	39.8	<u>46.7</u>	55.2	5.4		39.2	<u>45.3</u>	48.8	3.4
ASIn1	2.31	<u>2.54</u>	2.76	0.16		1.55	<u>1.80</u>	2.06	0.14
ASIn2	2.18	<u>2.48</u>	2.87	0.19		1.56	<u>1.84</u>	2.15	0.19
ASIn3	2.04	<u>2.46</u>	2.89	0.22		1.42	<u>1.73</u>	2.13	0.22
ASIn4	1.82	<u>2.15</u>	2.45	0.20		1.33	<u>1.70</u>	1.91	0.19
ASC1	62	<u>73</u>	84	7		80	<u>94</u>	107	8
ASC2	64	<u>79</u>	96	9		90	<u>109</u>	116	9
ASC3	70	<u>91</u>	109	12		114	<u>124</u>	132	6.6
ASC4	116	<u>134</u>	164	15		122	<u>141</u>	156	11

0.49–0.62–0.82 (SD, 0.10). Sucker dentition: half inner ring circumference with 6–7 blunt projections, half circumference with 6–7 pointed teeth (Figure 12B); infundibulum with 8–9 rings of round-ovate processes without pegs; at periphery processes smaller, flattened, hexagonal, or quadrilateral (Figure 10D). Swimming keel of club extends slightly beyond carpus (Figure 12A). Dorsal and ventral protective membranes not

fused at base of club; joined to stalk; differ in length, ventral protective membrane terminates at posterior end of carpus, dorsal membrane shorter than carpus (Figure 12A); approximately equal width; dorsal protective membrane forms shallow cleft at junction with stalk.

Gills with 20–25 lamellae per demibranch; females with greater number than males; GiLC males 20–21–22 (SD, 1), females 23–24–25 (SD, 1).

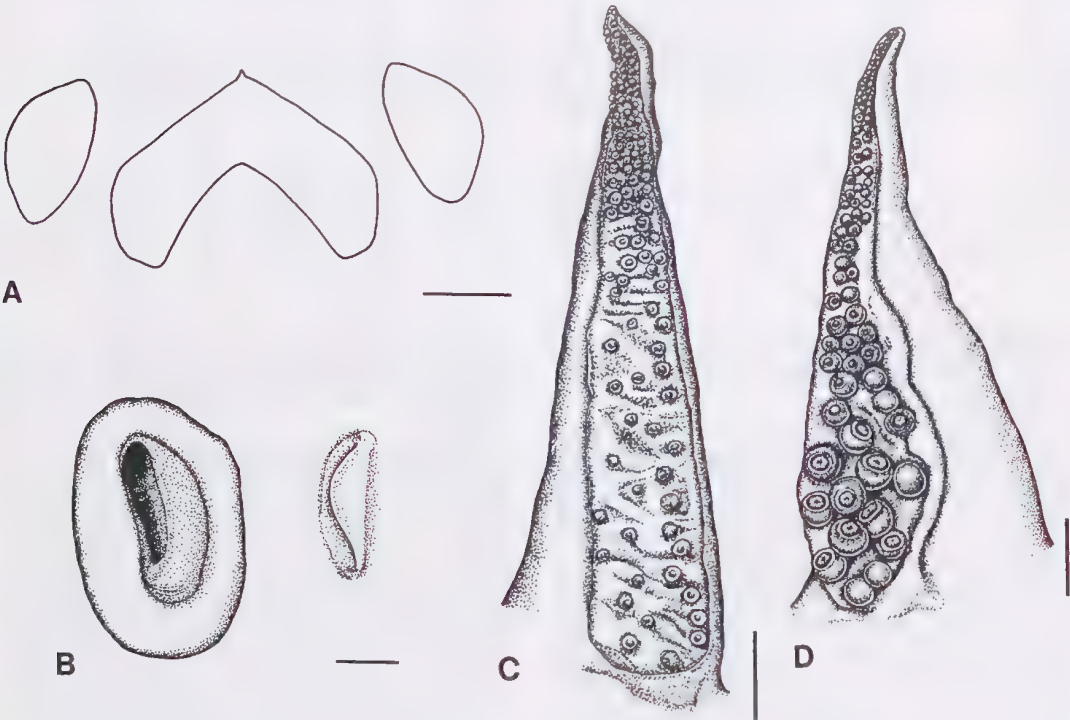


Figure 11 *Sepia senta* sp. nov.; A, funnel organ, male holotype MV F77200, 41.5 mm ML; B, funnel-locking cartilage (left), and mantle-locking cartilage (right), male holotype MV F77200, 41.5 mm ML; C, hectocotylied left ventral arm, male paratype WAM 332–86, 57.3 mm ML; D, right ventral arm, male paratype WAM 332–86, 57.3 mm ML. Scale bars 2 mm.

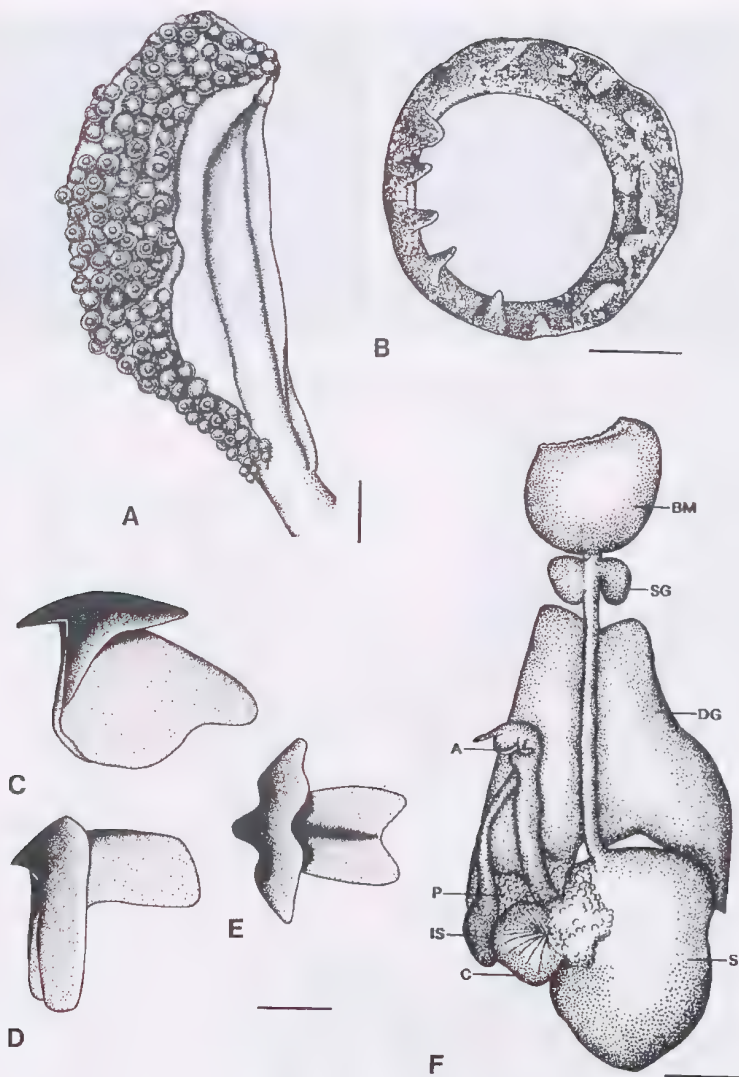


Figure 12 *Sepia senta* sp. nov.; A, tentacular club, female MV F77201, 75.3 mm ML, scale bar 2 mm; B, club sucker infundibulum, female paratype MV F77197, 48.2 mm ML, scale bar 50 µm; C, upper beak, lateral view; D, lower beak, lateral view; E, lower beak, ventral view (C–E, female paratype MV F77195, 64.2 mm ML, scale bar 2 mm); F, digestive tract, dorsal view, female MV F77196, 58.6 mm ML, scale bar 5 mm, abbreviations as in Figure 5E.

Gill length: GILI males 21.8–32.5–41.2 (SD, 6.3), females 26.1–34.9–40.9 (SD, 4.4).

Buccal membrane without suckers. Upper beak (Figure 12C) rostrum sharply pointed, long, length greater than width, cutting edge straight; hood high above crest posteriorly; crest curved, lateral wall shallowly indented posteriorly; wings and hood narrow and short; jaw angle approximately 90°, slightly acute; hood dark brown, lighter on ventral margin, crest only slightly pigmented. Lower beak (Figure 12D,E) rostrum protrudes only slightly; cutting edge slightly curved; hood low on

crest; crest straight, no indentation on lateral wall edge; hood and wings, width narrow; hood notch deep, broad (Figure 12E); wings widely spaced; crest wide; rostrum pigmented dark brown, wings pigmented along margin, pigmentation on hood fades posteriorly, crest pigmented medially in narrow band. Radula with 7 teeth per row; homodont; rhachidian teeth with narrow, truncate bases, slender, triangular, sides straight to slightly concave (Figure 13A,B); first lateral teeth similar length to rhachidian teeth, slightly broader with wide heels, asymmetrical with mesocone displaced

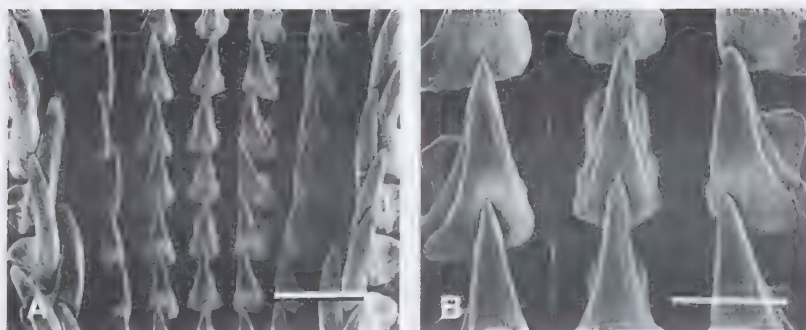


Figure 13 A–B, *Sepia senta* sp. nov.; A, radula, male holotype MV F77200, 41.5 mm ML, scale bar 200 µm; B, 1st lateral and rhachidian (centre) teeth, same specimen, scale bar 100 µm.

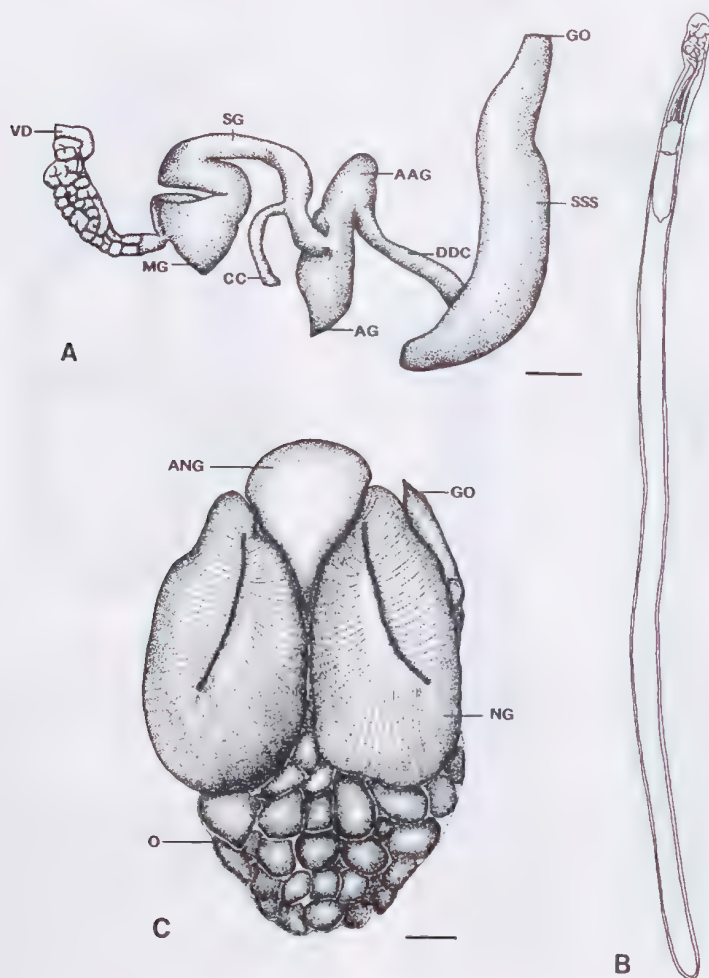


Figure 14 *Sepia senta* sp. nov.; A, male reproductive tract (testis not shown), paratype MV F77197, 49.8 mm ML, scale bar 2 mm, abbreviations as in figure 6A; B, spermatophore, male paratype MV F77197, 49.8 mm ML, scale bar 1 mm; C, female reproductive tract, paratype WAM 104–96, 83.2 mm ML, scale bar 5 mm, abbreviations as in Figure 6C.

toward centre of radula (Figure 13A,B); second laterals longer than first, distinctly curved, with broad heels; marginal teeth elongate with long tapered and curved mesocone (Figure 13A). Digestive tract (Figure 12F): paired salivary glands approximately one-third length of buccal mass; paired digestive glands large, located close together, with sub-triangular lobes posteriorly, ducts (not shown in figure) connect digestive glands near midline with caecum, ducts with branched attached pancreatic tissue; oesophagus runs dorsally along median junction of digestive glands, joins sac-like stomach immediately posterior to digestive gland; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens opens into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland (Figure 14A). Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joins spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophore storage sac; genital orifice opens dorsal to left gill in anterior end of mantle cavity. Spermatophores: cement body bipartite (Figures 14B, 15A,B); aboral end elongate, cylindrical, connects to sperm reservoir via narrow duct which extends from nipple-like tip of cement body; oral end of cement body approximately half length of, and slightly narrower than aboral end; connects to aboral end via narrow neck, tapers toward oral extremity of cement body; middle tunic commences along aboral part of cement body; ejaculatory apparatus coiled, extends into oral dilation of spermatophore. Spermatophores 4.8–5.6–6.5 mm long (SD, 0.5), 0.15–0.20–0.30 mm wide (SD, 0.04); SpLI 8.9–10.6–13.3 (SD, 1.4); SpWI 2.73–3.59–4.17 (SD, 0.39).

Female reproductive tract: ovary hangs from dorsal wall of posterior viscero-pericardial coelom. Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands, in mature animals occupy large portion of ventral side of mantle cavity. Accessory nidamental glands anterior to nidamental glands (Figure 14C). Eggs spherical 3.6–4.6–5.6 mm diameter (SD, 0.9); EgDI 5.5–6.6–8.3 (SD, 1.2).

Subdermal cartilaginous layer between cuttlebone and skin absent. Cuttlebone length approximately equal to mantle length; outline oval; CbL males 47.0–54.0–59.4 (SD, 4.2), females 43.3–60.7–75.4 (SD, 9.7); CbWI males 42.4–46.1–49.1 (SD, 2.3), females 43.0–46.5–50.8 (SD, 2.9); triangular, obtuse anteriorly; bluntly rounded posteriorly



Figure 15 A–B, *Sepia senta* sp. nov.; A, oral end of spermatophore, paratype MV F77197, 49.8 mm ML, scale bar 400 µm; B, enlargement of middle portion of ejaculatory apparatus, same specimen, scale bar 200 µm.

(Figure 16A,B). Dorsal surface yellowish; flat medially, curved, convex laterally; texture rough, with irregular calcified projections (particularly pronounced towards distal tip of sepium) (Figure 16C–E). Dorsal median rib present, indistinct, broadens anteriorly; lateral ribs present, indistinct. Dorso-posterior end of cuttlebone without median longitudinal ridge. Chitin present as a thin flim over entire dorsal surface of cuttlebone. Spine absent (Figure 16D). Striated zone flat; StZI males 50.3–56.5–60.6 (SD, 3.0), females 45.5–51.2–55.9 (SD, 3.4). Last locus convex; LoLI males 36.2–40.2–43.8 (SD, 2.2), females 40.5–46.5–50.8 (SD, 3.1). Last locus slightly shorter than striated zone, LoL/StZ(%) males 61.8–71.4–81 (SD, 6.4), females 72.4–91.3–102.8 (SD, 10.4). Sulcus absent. Anterior striae slightly convex to straight (Figure 16B). Limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs uniform width, narrow, not raised to form ledge; not thickened posteriorly (Figure 16B,E). Outer cone calcified; broadens slightly posteriorly (Figure 16B); lateral limbs not flared, slightly recurved posteriorly (Figure 16E).

Body papillae absent. Head and arm papillae absent. Colour (alcohol preserved specimens): head

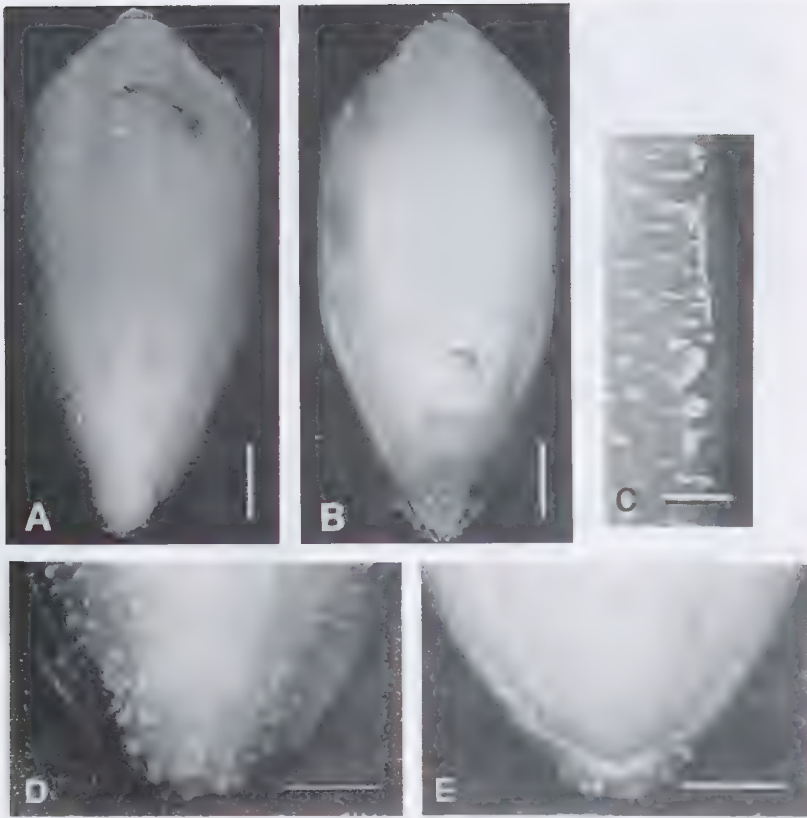


Figure 16 A–E, *Sepia senta* sp. nov.: A, cuttlebone, dorsal view, female paratype MV F77197, 48.2 mm ML, scale bar 7 mm; B, cuttlebone ventral view, same specimen, scale bar 7 mm; C, lateral margin of cuttlebone, dorsal view, female MV F77198, 60.7 mm ML, scale bar 4 mm; D, posterior end of cuttlebone, dorsal view, male paratype MV F77197, 49.8 mm ML, scale bar 1 mm; E, posterior end of cuttlebone, ventral view, male paratype MV F77197, 49.8 mm ML, scale bar 5 mm.

and arms pale, without colour pattern; dorsal mantle pale brownish, without markings (Figure 10A); paired dorsal eye spots absent. Fins pale; without markings at base. Arms without markings. Ventral pigment absent (Figure 10B).

Type locality

Australia: Western Australia, North West Shelf, 14°07'S 122°06'E; 415 m.

TYPE: Holotype, MV F77200, male 41.5 mm ML.

Distribution

Australia: Western Australia, North West Shelf, 12°04'S 122°51'E – 18°44'S 116°59'E (Figure 9); depth range 426–256 m. Habitat soft, muddy substrate.

Etymology

The specific name, *senta*, is derived from the Latin, *sentus*, meaning “thorny or rough”. It refers

to the calcareous protuberances on the dorsal side of the cuttlebone in this species. Gender feminine.

Remarks

A single male animal (MV F77982) from off Cebu in the Philippines (14°41.07'N 123°24.12'E – 14°42.42'N – 123°21.42'E) closely resembles this species. The specimen differs, however, in a number of morphometric characters, notably in having relatively shorter arms, smaller arm and club suckers and a greater number of gill lamellae and rows of club suckers than the Australian animals. Measurements, counts and indices for this specimen are shown in Table 4 for comparison. The left ventral arm of the Philippines specimen shows no modification, but as it additionally has no mature spermatophores in the spermatophore storage sac, the animal may be immature. The body pigmentation is much darker, a deep rust brown in the Philippines animal, in contrast to the pale brownish skin coloration of the Australian

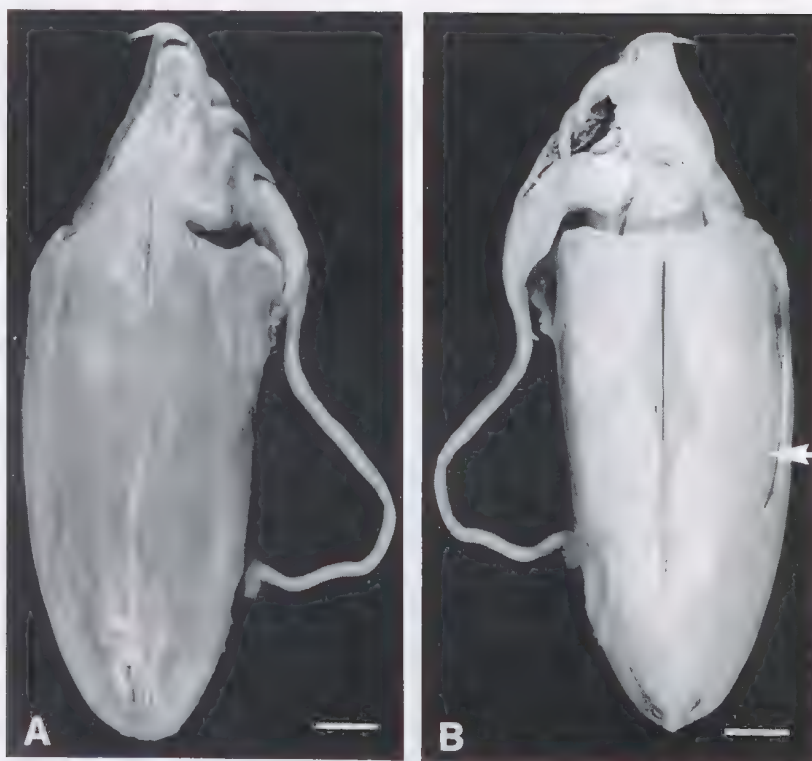


Figure 17 A–B, *Sepia sulcata* Hoyle; A, dorsal view female MV F56919, 96.2 mm ML; B, ventral view, same specimen, arrow indicates the position of a ventrolateral ridge. Scale bars 10 mm.

animals. The dorsal surface of the sepioid is roughened with calcified projections, but these projections are more regular in arrangement and shape in the Philippines animal than in the Australian species. The Philippines animal was collected at 30 m depth, in contrast to the Australian specimens found between 426–256 m. Until additional specimens become available, conspecificity of the Philippines form with *S. senta* sp. nov. remains uncertain.

Sepia senta sp. nov. differs from all other sepioids in the structure of the dorsal side of the cuttlebone, with its irregular calcareous projections. Other characters are either shared or differ among other members of the genus. As discussed in the remarks section of *S. plana* above, until relationships among the sepioids are established there is little value in comparing differences in individual characters between *S. senta* sp. nov. and all other nominal species.

Sepia sulcata Hoyle, 1885
Figures 9, 17–25; Tables 7–10

Holotype

Indonesia: Arafura Sea, off Ki Is. – 1M (53.2 mm

ML), 5°49'15"S 132°14'15"E, 140 fms (255 m), 26 Sep 1874, coll. W.E. Hoyle on HMS "Challenger", (BMNH 89.4.24.77).

Additional material

Australia: Western Australia, North West Shelf – 2F (28.1, 38.1 mm ML), NW of Augustus Is., 13°51.4'S 123°01.8'E – 13°52.8'S 122°59.0'E, 308–306 m, 14 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 337–86); 1F (42.8 mm ML), NW of Collier Bay, 14°16.5'S 122°34.4'E – 14°13.6'S 122°38.3'E, 302 m, 14 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 336–86); 3F (57.0–64.1 mm ML), NW of Augustus Is., 14°29.4'S 122°01.4'E – 14°28.4'S 122°03.2'E, 304–296 m, 12 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 335–86); 7M (37.8–50.6 mm ML) 13F (37.1–65.3 mm ML), 14°35.8'S 121°49.4'E – 14°37.2'S 121°47.4'E, 304–300 m, 16 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 343–86); 6M (42.9–60.0 mm ML) 4F (55.6–66.1 mm ML), NW of Cape Leveque, 14°49.0'S 121°31.1'E – 14°50.8'S 121°35.6'E, 302–300 m, 12 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 333–86); 4M (46.0–52.7 mm ML) 2F (42.8, 60.9 mm ML), NW of Cape Leveque, 14°51.9'S 121°40.6'E, 260–256 m, 16 Feb 1984, coll. S. Slack-Smith on RV "Soela",

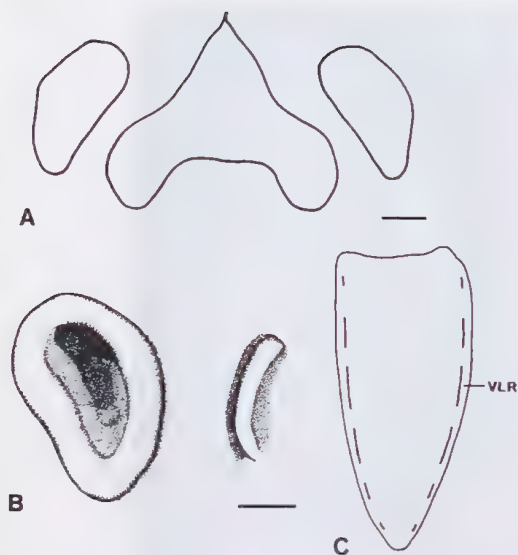


Figure 18 A–B, *Sepia sulcata* Hoyle; A, funnel organ, female MV F56919, 96.2 mm ML, scale bar 2 mm; B, funnel-locking cartilage (left), and mantle-locking cartilage (right), male MV F56919, 65.9 mm ML, scale bar 2 mm; C, diagram of mantle, ventral view showing position of ventrolateral ridges (VLR).

(WAM 339–86); 1M (45.7 mm ML) 5F (45.1–61.3 mm ML), NW of Cape Leveque, 15°11.1'S 121°26.9'E – 15°12.9'S 121°25.7'E, 260–258 m, 17 Feb 1984, coll. S. Slack-Smith on RV "Soela", (WAM 341–86); 5F (35.9–56.9 mm ML), North West Shelf, 18°10'S 118°18'E – 18°10'S 118°23'E, 300–298 m, 10 May 1982, coll. RV "Courageous", (MV F65584); 2M (65.9, 67.6 mm ML) 2F (86.6, 96.2 mm ML), North West Shelf, 18°49'S 117°41'E, 168–166 m, 6 May 1983, coll. RV "Soela", (MV F56919); 1F (90.6 mm ML), North West Shelf, 18°36'S 118°2'E, 184–182 m, 6 Jun 1983, coll. RV "Soela", (MV F56918); 1M (38.5 mm ML) 2F (54.5, 64.1 mm ML), off Port Headland, 18°41'S 117°54'E – 18°41'S 117°52.6'E, 404 m, 2 Apr 1982, coll. L. Marsh on RV "Soela", (WAM 3103–83); 1M (62.8 mm ML) 2F (61.5, 67.2 mm ML), off Port Headland, 18°54'S 117°02'E – 18°55.5'S 117°00'E, 306–300 m, 13 Apr 1982, L. Marsh on RV "Soela", (WAM 3102–83); 1F (85.7 mm ML), N of Monte Bello Is., 19°58'S 115°13'E, 180–150 m, 10 May 1978, coll. RV "Courageous", (WAM 3100–83).

Diagnosis

Sucker rows on arms 1–3 in males biserial proximally (approximately 8–11 rows biserial suckers arms 1, 6–8 rows biserial suckers arms 2 and 3), tetraserial distally; suckers arms 4 biserial proximally (approximately 2 rows), tetraserial

distally. Sucker rows on arms 1–3 in females biserial proximally for 6–7 rows, tetraserial distally, suckers on arms 4 biserial proximally for 2–3 rows, rest tetraserial. Distal arm tips strongly attenuate. A thick, cartilaginous sub-dermal layer adheres closely to dorsal side of cuttlebone. Cuttlebone oblong, strongly acuminate, acute anteriorly and posteriorly. Dorsal median and lateral ribs present, distinct. Sulcus shallow, narrow, flanked by prominent rounded ribs bordered laterally by shallow grooves. Inner cone limbs form narrow, raised ledge posteriorly. Left ventral arm hectocotylised: proximally 14 rows (approximately) of greatly reduced suckers; 2 dorsal and 2 ventral series widely spaced; in mature males, oral surface wide, fleshy with deep longitudinal furrow between swollen protective membranes. Tentacular clubs with 5–7 small, subequal suckers in transverse rows; dorsal and ventral protective membranes not fused at base of club. Dorsal mantle with up to 10 short, longitudinal, orange-pink ridges along each side close to fins; ventral mantle with 6 (3 long and 3 short) longitudinal ridges along each side close to fins. Small to moderate sized species, maximum size up to approximately 100 mm ML.

Description

Counts and indices for individual specimens are given in Table 7–8; ranges for arm length indices, arm sucker diameter indices and arm sucker counts are shown in Table 9.

Small to moderate sized species; ML males 42.9–55.7–67.6 mm (SD, 8.1), females 61.3–74.6–96.2 mm (SD, 13.5). Mantle very slender, obovate; MWI males 40.4–45.3–51.7 (SD, 2.9), females 39.3–45.0–51.6 (SD, 4.2); markedly attenuate posteriorly, tapers to point (Figure 17A,B); dorsal anterior margin triangular, acute (Figure 17A); projects anteriorly beyond eyes; AMHI males 12.8–14.6–16.6 (SD, 1.1), females 12.5–14.7–16.2 (SD, 1.2). Ventral mantle margin emarginate, without distinct lateral angle; VMLI males 81.2–86.9–95.8 (SD, 4.4), females 69.8–83.5–88.7 (SD, 5.7). Fins widest in posterior third; FWI males 5.8–8.6–11.2 (SD, 1.7), females 5.0–8.6–11.1 (SD, 2.1); anterior origin posterior to mantle margin; FIIa males 5.1–6.8–8.9 (SD, 1.2), females 2.5–5.6–8.7 (SD, 2.0); rounded posteriorly; narrow gap between fins; FIIP males 6.8–8.2–9.8 (SD, 1.0), females 4.1–6.8–9.2 (SD, 1.7). Funnel long, broad-based; extends to anterior rim of eye; FuLI males 23.9–29.4–32.6 (SD, 3.2), females 26.4–29.9–31.8 (SD, 1.9). Funnel free portion approximately half funnel length, FFuI males 8.8–12.2–18.8 (SD, 2.7), females 26.4–29.9–31.8 (SD, 1.9). Funnel organ dorsal elements inverted V-shape with small papilla in front; ventral elements oval (Figure 18A). Mantle-locking cartilage curved, with semicircular ridge; funnel-locking cartilage with

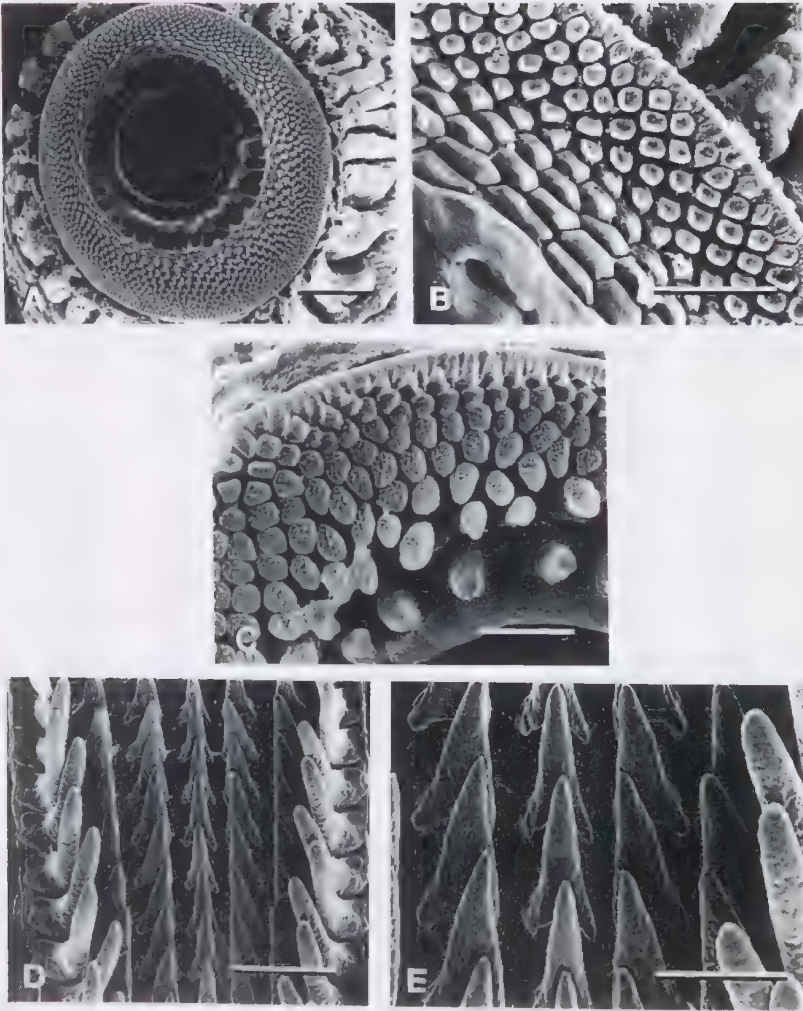


Figure 19 A–E, *Sepia sulcata* Hoyle; A, sucker rim, arm 2, male MV F56919, 65.9 mm ML, scale bar 100 µm; B, sucker rim, arm 2, female MV F56919, 96.2 mm ML, scale bar 30 µm; C, club sucker rim, female MV F56919, 96.2 mm ML, scale bar 30 µm; D, radula, female MV F56919, 96.2 mm ML, scale bar 200 µm; E, radula, from left to right 1st laterals, rhachidian, 1st and 2nd lateral teeth, marginal teeth (distal tips) same specimen, scale bar 200 µm.

depression which corresponds to ridge (Figure 18B). Head slender; HLI males 20.6–25.6–29.6 (SD, 2.8), females 16.1–23.2–31.9 (SD, 4.5); narrower than mantle; HWI males 29.0–35.3–41.7 (SD, 3.8), females 28.9–35.6–40.9 (SD, 4.2). Eyes moderate size, EDI males 11.2–12.5–14.9 (SD, 1.2), females 8.6–11.2–14.1 (SD, 1.5); ventral eyelids present.

Male and female arms subequal in length (Table 9). ALI of longest arms in male 30.4–36.4–42.5 (SD, 4.0), females 32.7–35.3–39.1 (SD, 2.2). Protective membranes (both sexes) wide, well developed; normal, not thickened. Distal arm tips (both sexes) strongly attenuate, suckers enclosed by protective membranes. Arrangement of arm sucker rows

differs between sexes. In males, sucker rows on arms 1–3 biserial proximally (approximately 8–11 rows biserial suckers arms 1, 6–8 rows biserial suckers arms 2 and 3), tetraserial distally; arms 4 suckers biserial at base (approximately 2 rows), suckers tetraserial distally. In females, sucker rows on arms 1–3 biserial proximally for 6–7 rows, tetraserial distally; suckers on arms 4 biserial proximally for 2–3 rows, rest tetraserial. Suckers in males normal in size (not greatly enlarged); larger than female arm suckers (Table 9). Chitinous rims of arm suckers smooth, or with blunt processes on inner ring; infundibulum with 9–13 rows of ovoid-hexagonal processes with blunt pegs, inner row

Table 7 *Sepia sulcata* Hoyle; measurements (mm), counts and indices of 10 mature males.

Museum Reg. No.	BMNH 89.4.24.77 (Holotype)	WAM 333-86	WAM 343-86	WAM 343-86	WAM 339-86	WAM 333-86	WAM 333-86	WAM 3102-83	MV F56919	MV F56919
ML	53.2	42.9	47.8	50.6	52.7	53.9	60.0	62.8	65.9	67.6
MWI	46.4	51.7	46.2	44.7	46.3	45.5	45.2	40.4	43.4	43.6
AMHI	14.1	16.1	13.8	12.8	15.0	14.3	14.5	16.6	14.6	14.5
VMLI	86.8	95.8	86.2	93.1	84.3	86.1	87.0	81.2	85.1	83.9
FWI	9.4	9.8	9.8	8.9	7.6	7.6	5.8	6.5	9.3	11.2
FIla	5.1	8.2	7.7	7.3	8.9	6.9	6.0	6.4	5.3	6.1
FIIp	8.5	8.2	9.8	8.3	7.6	7.8	8.3	7.2	6.8	9.6
FuLI	32.5	32.6	32.4	23.9	24.7	29.7	28.3	28.7	32.6	28.7
FFuI	18.8	11.7	13.6	9.9	11.4	12.1	11.7	8.8	11.4	12.6
HLI	27.8	29.6	26.6	28.1	23.3	20.6	25.5	23.4	-	25.9
HWI	41.7	35.2	41.0	33.2	33.2	35.6	34.7	33.0	36.4	29.0
EDI	12.0	12.4	14.9	11.3	11.2	11.7	13.7	12.6	11.7	13.6
ALI1	30.1	33.8	31.4	33.6	31.3	39.0	33.3	34.2	37.2	38.5
ALI2	30.1	32.6	33.5	31.6	36.1	30.6	29.2	28.7	33.4	35.5
ALI3	28.2	32.6	31.4	32.6	30.4	33.4	33.3	30.3	33.4	36.2
ALI4	32.0	42.0	35.6	38.5	30.4	36.0	38.3	33.4	42.5	35.5
ASIn1	1.07	1.40	1.26	1.48	1.35	1.11	1.25	1.27	1.32	1.33
ASIn2	1.17	1.17	1.26	1.48	1.35	1.11	1.33	1.19	1.32	1.36
ASIn3	0.94	1.52	1.26	1.58	1.40	1.11	1.42	1.35	1.52	1.48
ASIn4	1.17	1.63	1.36	1.68	1.54	1.48	1.50	1.53	1.78	1.66
ASC1	-	76	88	110	94	106	86	94	102	106
ASC2	92	90	106	104	-	114	80	104	124	127
ASC3	94	88	108	102	104	96	106	96	113	126
ASC4	104	120	140	146	150	152	140	-	140	120
ASIn14	0.70	0.93	0.63	0.79	0.66	0.93	0.75	0.83	1.02	0.96
ASIn14m	0.51	0.58	0.52	0.59	0.38	0.56	0.33	0.51	0.38	0.40
CILI	11.3	14.0	13.0	-	10.6	9.8	9.3	14.3	10.2	10.4
CIRC	7	5	5	-	6	5	5	5	5	5
TrRC	19	21	21	-	24	18	18	22	23	22
CISI	0.51	0.58	0.46	-	0.57	0.46	0.52	0.57	0.56	0.70
CISId	0.47	0.47	0.42	-	0.42	0.41	0.47	0.51	0.46	0.44
CISlv	0.41	0.42	0.36	-	0.42	0.41	0.43	0.45	0.38	0.37
GiLC	29	27	27	27	26	27	26	27	29	29
GiLI	36.1	33.1	33.5	30.8	29.8	28.4	28.2	30.4	26.6	21.3
SpLI	-	11.7	8.4	9.5	11.4	9.8	9.3	10.7	12.4	12.6
SpWI	-	5.00	6.25	6.25	4.50	9.43	4.46	4.78	3.66	3.18
CbL	-	-	47	49	50.3	5.3	-	60.9	65	65.6
CbWI	-	-	34.0	34.1	33.0	32.3	-	31.2	29.4	31.3
SLI	-	-	-	-	-	4.4	-	2.5	3.1	3.2
StZI	-	-	63.4	63.1	60.2	60.0	-	64.2	65.7	67.8
LoLI	-	-	35.1	36.9	38.2	40.3	-	33.7	28.9	31.7
LoL/StZ (%)	-	-	55.4	58.6	63.4	67.2	-	52.4	44.0	46.7

processes larger than rest, rectangular; peripheral sucker rim processes radially arranged, elongate, without pegs (Figure 19A,B). Sucker counts range from 76–152; females with higher average counts than males (Table 9).

Left ventral arm hectocotylised. Suckers: reduced proximally in size: 14 rows of suckers reduced (approximately, dorsal and ventral sides of hectocotylus differ, see Figure 20); suckers in dorsal marginal series smaller than remaining suckers (Figure 20 A,B, compare with Figure 20C); reduction marked, maximum and minimum sucker diameters: ASIn14 0.63–0.82–1.02 (SD, 0.14), ASIn14m 0.33–0.48–0.59 (SD, 0.09), (compare with

non-hectocotylised arms Table 9); two dorsal and two ventral series of suckers widely spaced. Oral surface wide, fleshy, with transversely grooved ridges; proximal end with deep furrow between raised fleshy ridge formed from swollen protective membranes; distal to this region, protective membranes thin, wide, form a deep, narrow furrow (Figure 20B). Hectocotylised arm distally attenuate, compressed (as for remaining arms).

Tentacular club approximately same length in males and females; CILI males 9.3–11.4–14.3 (SD, 1.9), females 9.8–11.2–14.9 (SD, 1.6); club crescent-shaped (very short); sucker-bearing face flattened. Club with 5–7 suckers in transverse rows, CIRC

Table 8 *Sepia sulcata* Hoyle; measurements (mm), counts and indices of 10 mature females

Museum Reg. No.	WAM 341–86	WAM 3102–83	WAM 343–86	WAM 343–86	WAM 333–86	WAM 3102–83	WAM 3100–83	MV F56919	MV F56918	MV F56919
ML	61.3	61.5	65.1	65.3	66.1	67.2	85.7	86.6	90.6	96.2
MWI	48.9	44.6	42.2	50.7	43.1	51.6	45.5	41.0	42.7	39.3
AMHI	16.0	14.0	13.8	15.0	13.8	15.6	16.2	15.7	13.9	12.5
VMLI	85.0	82.9	85.4	78.7	88.7	82.6	69.8	88.0	86.6	87.5
FWI	7.7	7.8	8.0	–	10.1	6.4	5.0	11.1	10.5	10.7
FIHa	6.2	6.8	4.8	8.7	6.1	8.2	4.2	4.3	4.2	2.5
FIHp	8.0	7.0	4.6	7.4	7.7	8.0	5.0	6.7	9.2	4.1
FuLI	31.8	28.9	31.2	31.4	31.0	28.3	26.4	27.7	30.9	31.7
FFuI	11.4	8.9	10.0	12.3	11.3	16.4	12.8	13.9	15.5	16.1
HLI	26.3	24.2	–	31.9	20.3	16.1	24.4	19.1	23.1	23.9
HWI	36.5	33.8	–	36.0	38.9	40.9	40.5	30.1	34.8	28.9
EDI	12.2	10.4	–	14.1	11.2	8.6	10.5	11.5	11.9	10.6
ALI1	32.6	32.5	29.2	38.3	34.0	30.5	31.5	34.6	34.8	33.8
ALI2	30.2	30.9	26.1	34.5	31.8	26.0	30.3	30.6	34.8	33.3
ALI3	28.5	30.9	29.2	33.7	31.8	27.5	31.5	31.2	33.1	31.2
ALI4	33.4	34.1	36.9	39.1	34.8	32.7	33.8	33.5	36.4	37.9
ASIn1	0.98	1.38	1.08	1.07	1.21	1.56	1.12	1.15	1.27	1.04
ASIn2	1.04	1.46	1.15	1.07	1.21	1.19	1.12	1.21	1.24	1.16
ASIn3	1.04	1.46	1.15	1.07	1.13	1.34	1.05	1.15	1.24	1.14
ASIn4	0.98	1.63	1.23	1.23	1.21	1.19	1.05	1.15	1.10	1.16
ASC1	95	102	106	112	96	90	120	98	106	100
ASC2	124	102	116	128	104	126	106	114	130	126
ASC3	136	110	136	128	144	132	112	122	120	117
ASC4	152	–	142	152	132	145	130	132	103	144
CILI	10.4	9.8	10.1	11.5	10.6	14.9	11.1	10.3	12.7	10.2
CIRC	5	5	5	5	5	7	5	5	5	5
TrRC	21	22	21	21	21	20	22	22	22	22
CISI	0.46	0.60	0.61	0.61	0.61	0.54	0.64	0.60	0.55	0.52
CISId	0.39	0.50	0.46	0.57	0.48	0.54	0.41	0.46	0.46	0.47
CISlv	0.39	0.41	0.40	0.54	0.53	0.40	0.35	0.46	0.46	0.36
GiLC	27	27	27	27	28	–	–	31	31	–
EgDI	–	–	–	–	–	–	–	4.0	4.3	4.6
GiLI	28.7	29.8	29.0	34.6	29.8	33.8	28.8	26.7	27.0	32.2
CbL	61.3	60.5	63.3	62.7	64.4	65.6	80.1	86.5	–	–
CbWI	33.0	32.1	33.2	31.9	33.7	33.1	30.0	28.7	–	–
SLI	3.3	3.3	3.5	3.3	3.4	–	2.5	1.2	–	–
StZI	60.2	65.3	57.0	63.3	61.3	–	71.3	69.7	–	–
LoLI	39.2	33.6	37.9	36.8	38.0	–	25.0	25.3	–	–
LoL/StZ (%)	65.0	51.4	66.5	58.2	62.0	–	35.0	36.3	–	–

males 5–5–6 (SD, 0), females 5–5–7 (SD, 1); 18–24 suckers in longitudinal series, TrRC males 18–21–24 (SD, 2), females 20–21–22 (SD, 1). Suckers differ slightly in size (Figure 21A); small (those in middle of club slightly larger than rest); CISI males 0.46–0.55–0.7 (SD, 0.07), females 0.46–0.57–0.64 (SD, 0.06); dorsal marginal series of suckers slightly larger than those in ventral marginal series; CISId males 0.41–0.45–0.51 (SD, 0.03), females 0.39–0.47–0.57 (SD, 0.05); CISlv males 0.36–0.40–0.45 (SD, 0.03), females 0.35–0.43–0.54 (SD, 0.06). Sucker dentition: inner ring with approximately 20 elongate projections (Figure 19C) evenly distributed around circumference; infundibulum with 6–8 rows hexagonal-ovate processes without pegs; at periphery, processes smaller, flattened, hexagonal (Figure 19C). Swimming keel of club

extends beyond carpus for about third the length of the club (Figure 21A). Dorsal and ventral protective membranes not fused at base of club; joined to stalk; dorsal and ventral membranes differ in length, dorsal membrane extends beyond carpus along stalk, ventral membrane terminates at posterior end of carpus; dorsal membrane much wider than ventral membrane; dorsal membrane forms deep cleft at junction with stalk.

Gills with 26–31 lamellae per demibranch; GiLC males 26–27–29 (SD, 1), females 27–28–31 (SD, 2). Gill length: GiLI males 21.3–29.8–36.1 (SD, 4.1), females 26.7–30–34.6 (SD, 2.7).

Buccal membrane without suckers. Upper beak with long, pointed, and slightly curved rostrum, width greater than length (Figure 21B); cutting edge straight; hood high above crest posteriorly;

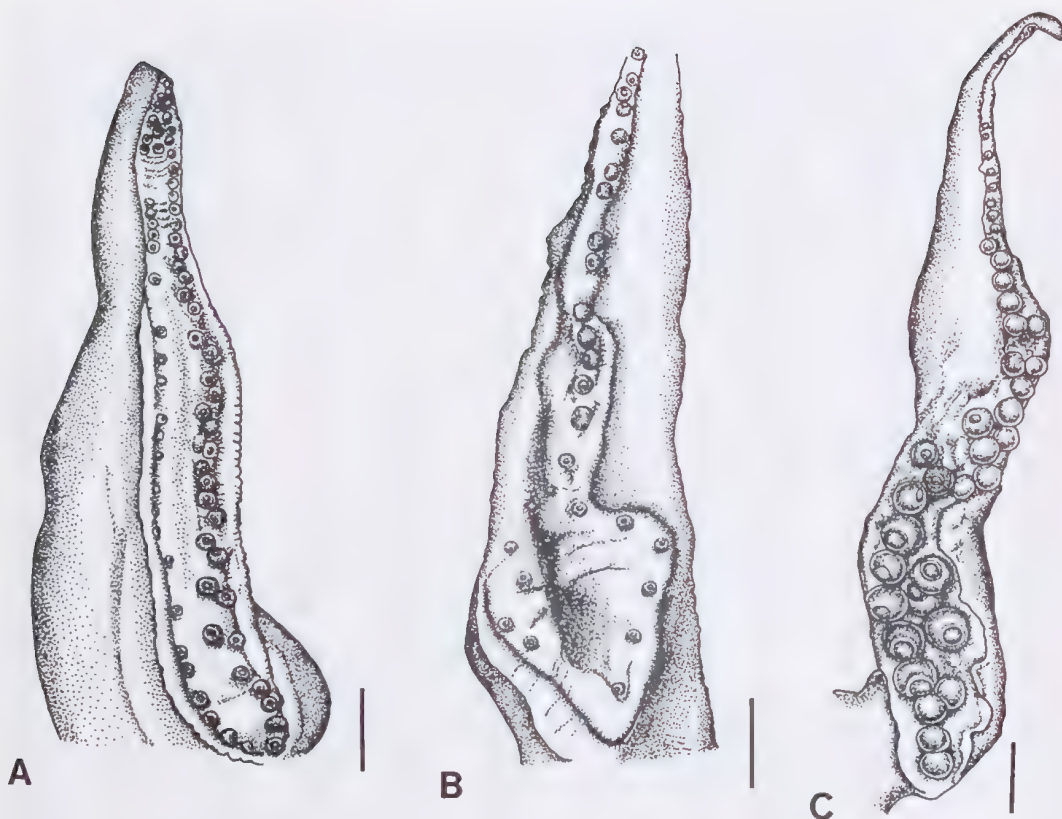


Figure 20 A–C, *Sepia sulcata* Hoyle; A, hectocotylied left ventral arm, holotype BMNH 89.4.24.77, 53.2 mm ML; B, modified portion of hectocotylied left ventral arm, MV F56919, 67.6 mm ML; C, right ventral arm, male MV F56919, 67.6 mm ML. Scale bars 2 mm.

wings and hood narrow and short; lateral wall shallowly indented posteriorly; jaw angle approximately 90°; hood darkly pigmented, fades toward posterior margin; crest pigmented along midline, lateral walls pale. Lower beak cutting edge straight; hood low on crest (Figure 21C); crest straight; lateral wall edge without indentation; hood and wings, width narrow; hood notch deep (Figure 21D); crest wide; jaw angle obtuse; hood darkly pigmented, fades toward posterior margin; crest pigmented along midline, lateral walls pale. Radula with 7 teeth per row; homodont; rhachidian teeth with broad, strongly indented bases, narrow, tapered, blunt distally (Figure 19D,E); first lateral teeth slightly longer, broader than rhachidian teeth, with wide heels and bases strongly indented, asymmetrical with mesocone displaced toward centre of radula (Figure 19D,E); second laterals similar in shape, slightly longer than first laterals; marginal teeth elongate, curved, bluntly rounded distally, with rounded heel, strongly indented proximally (Figure 19D). Digestive tract (Figure 21E): paired salivary glands approximately one-

third length of buccal mass; paired digestive glands large, located close together, with sub-triangular lobes posteriorly, ducts (not shown in figure) connect digestive glands near midline with caecum, with branched attached pancreatic tissue; oesophagus runs dorsally along median junction of digestive glands, joins sac-like stomach immediately posterior to digestive gland; caecum disc-like, grooved in blunt V-shape anteriorly, surface lining finely pleated; intestine undifferentiated; ink sac and anal flaps well developed.

Male reproductive tract: testis on left posterior side of viscero-pericardial coelom; at distal end, convoluted vas deferens (Figure 22A) opens into broad, cone-shaped mucilaginous gland, then narrower, curved, spermatophoric gland. Close to junction with lobe-shaped accessory gland and gland appendix, delicate ciliated canal joins spermatophoric gland; distal deferent canal connects appendix of accessory gland to spermatophore storage sac; genital orifice opens dorsal to left gill in anterior end of mantle cavity.

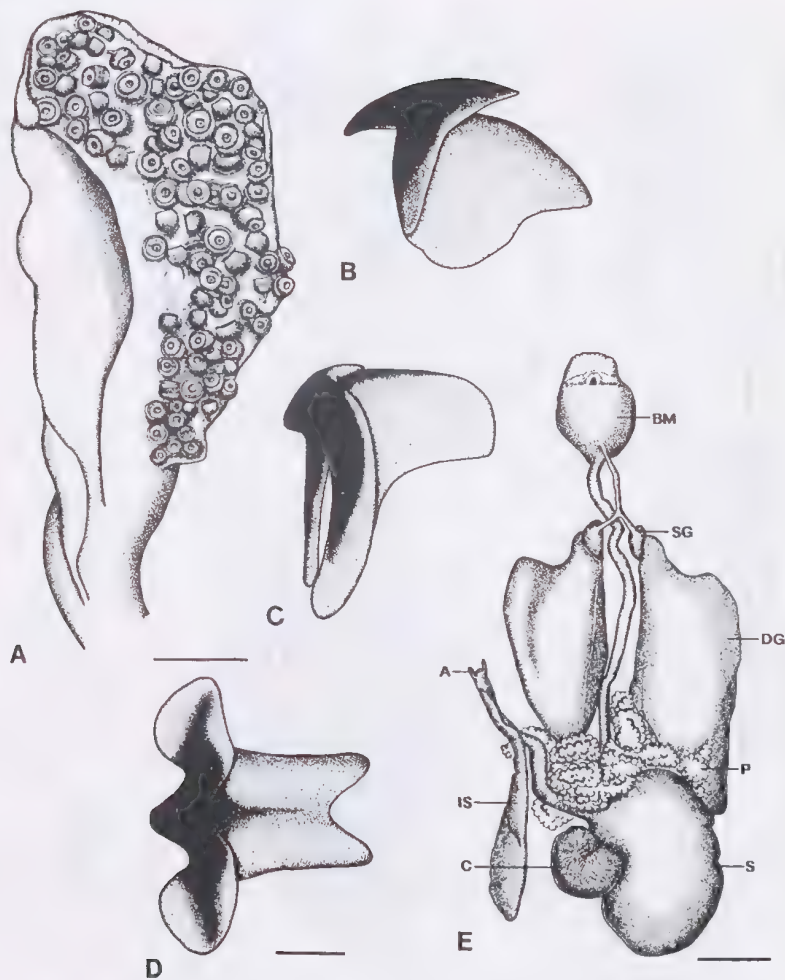


Figure 21 A–E, *Sepia sulcata* Hoyle; A, tentacular club, female WAM 341–86, 63.5 mm ML, scale bar 2 mm; B, upper beak, lateral view; C, lower beak, lateral view; D, lower beak, ventral view (B–D, male MV F56919, 65.9 mm ML, scale bar 2 mm); E, digestive tract, male WAM 333–86, 54.9 mm ML, scale bar 5 mm, abbreviations as in Figure 5E.

Table 9 *Sepia sulcata* Hoyle; ranges of arm length indices (ALI), arm sucker diameter indices (ASIn) and arm sucker counts (ASC) of 10 mature males and 10 mature females. min. = minimum, max. = maximum, SD = standard deviation.

	Males				Females			
	min.	mean	max.	SD	min.	mean	max.	SD
ALI1	30.1	<u>34.2</u>	39.0	3.1	29.2	<u>33.2</u>	38.3	2.5
ALI2	28.7	<u>32.1</u>	36.1	2.5	26.0	<u>30.8</u>	34.8	3.0
ALI3	28.2	<u>32.2</u>	36.2	2.2	27.5	<u>30.9</u>	33.7	1.9
ALI4	30.4	<u>36.4</u>	42.5	4.0	32.7	<u>35.3</u>	39.1	2.2
ASIn1	1.07	<u>1.28</u>	1.48	0.12	0.98	<u>1.19</u>	1.56	0.18
ASIn2	1.11	<u>1.27</u>	1.48	0.11	1.04	<u>1.19</u>	1.46	0.12
ASIn3	0.94	<u>1.36</u>	1.58	0.20	1.04	<u>1.18</u>	1.46	0.13
ASIn4	1.17	<u>1.53</u>	1.78	0.17	0.90	<u>1.19</u>	1.63	0.17
ASC1	76	<u>96</u>	110	11	90	<u>103</u>	120	9
ASC2	80	<u>105</u>	127	16	102	<u>118</u>	130	11
ASC3	88	<u>103</u>	126	11	110	<u>126</u>	144	11
ASC4	104	<u>135</u>	152	16	103	<u>137</u>	152	15

Table 10 Species of *Sepia* found in northwestern Australian waters, distinguishing features and depth ranges (in Australian waters). Primary source of information Lu (in press a,b). + = present, - = absent, F = flattened, C = convex, * = bone very distinctive: lanceolate (*S. cottoni*), flattened dorsally and laterally (*S. plana*), dorsally rough with calcareous projections (*S. senia*); † = one specimen has been collected from Qld., North Stradbroke Island 27°35'S 153°27'E (Adam, 1979); ‡ = possibly also eastern Australia, see remarks, *Sepia plana*.

Species	Arm Sucker Rows	Hectocotylised Arm	Club Sucker-bearing Face	CIRC	Club Suckers relative sizes	Club Dorsal & Ventral Protective Membranes			Cuttlebone	Inner Cone	Limbs	Depth Range (m)	Distribution (Australian)
						separate	fused	broaden posteriorly			form a ledge posteriorly		
<i>S. cottoni</i> Adam, 1979	+	+	-	F	5	vary, some large	+	-	+	+	-*	122 - 114	W.A., Hassall Beach, 34°49'S 118°24'E - Broome, 17°31'S 121°27'E †
<i>S. elliptica</i> Hoyle, 1885	-	+	+	F	10 - 12	all similar, minute	small large specimens	+	-	-	+	142 - 16	W.A., Exmouth Gulf, 22°23'S 114°06'E - Qld., Capricorn Group, 23°30'S 152°00'E
<i>S. irvingi</i> Meyer, 1909	-	+	-	F	8	vary, some large	+	-	+	+	-	170 - 130	W.A., Cockburn Sound, 32°11'S 115°43'E - North West Shelf, 18°49'S 118°29'E
<i>S. latimans</i> Quoy & Gaimard, 1832	-	+	-	F	5 - 6	vary, some large	+	-	+	+	-	30 - 0	W.A., Shark Bay, 25°25'S 113°35'E to Qld., approx. 23°S
<i>S. opipara</i> (Iredale, 1926)	-	+	+	F	8	vary, some large	+	-	+	+	-	184 - 83	W.A., Dirk Hartog Is., 25°45'S 113°03'E to Qld., 26°57'S 151°45'E
<i>S. papuensis</i> Hoyle, 1885	+	+	-	F	5 - 6	vary, some large	small large specimens	+	+	-	-	155 - 17	W.A., Fremantle, 32°03'S 115°44'E to N.S.W., 36°35'S 150°16'E
<i>S. plaraonis</i> Erenberg, 1831	-	+	+	F	8	vary, some large	+	+	+	bulbous, shiny	-	102 - 25	W.A., Cape Le Grande, 33°55'S 122°30'E to Qld., Townsville, 19°16'S 146°41'E
<i>S. plana</i> sp. nov. this study	-	+	+	F	8 - 10	all similar, small	+	-	-	-	-*	505 - 396	W.A., North West Shelf, 12°04'S 122°59'E - 17°55'S 118°16'0E ‡
<i>S. senia</i> sp. nov. this study	-	+	+	F	6 - 8	differ slightly, small	+	-	-	-	-*	426 - 256	W.A., North West Shelf, 14°07'S 122°51'E - 18°44'S 116°59'E
<i>S. smithi</i> Hoyle, 1885	-	+	+	C	20	all similar, minute	+	+	+	+	+	138 - 33	W.A., Shark Bay, 25°25'S 113°35'E to Qld., Moreton Bay, 27°25'S 153°20'E
<i>S. sulcata</i> sp. nov. Hoyle, 1886	+	+	+	F	5 - 7	differ slightly, small	+	+	-	-	+	404 - 150	W.A., North West Shelf, 13°51.4'S 123°01.8'E - 19°58'S 115°13'E.

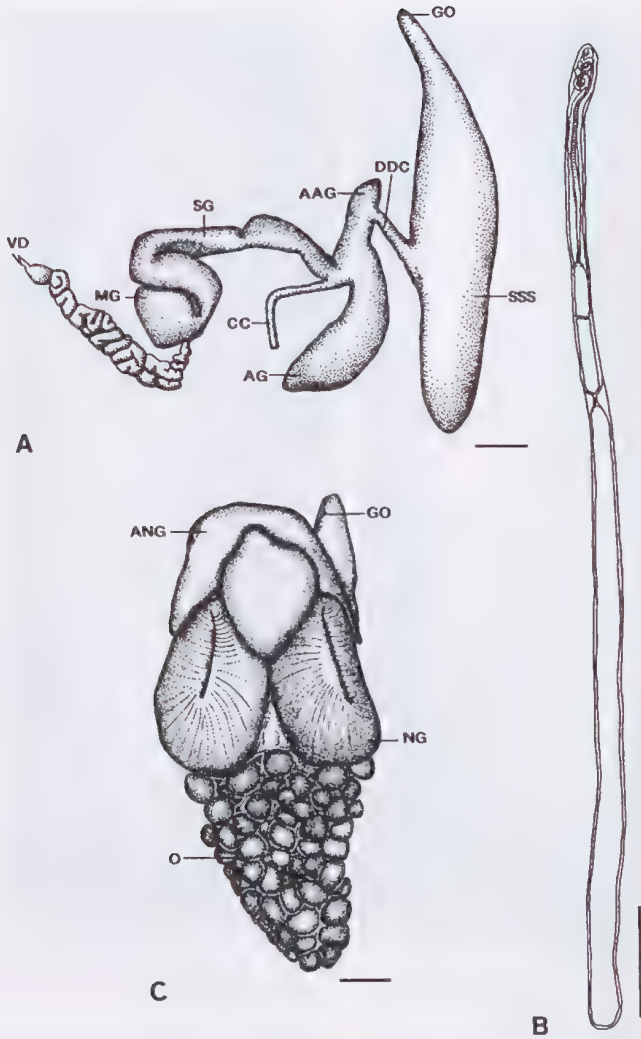


Figure 22 A–B, *Sepia sulcata* Hoyle; A, male reproductive tract (testis not shown), MV F56919, 65.9 mm ML, scale bar 1 mm, abbreviations as in Figure 6A; B, spermatophore, MV F56919, 67.6 mm ML, scale bar 1 mm; C, female reproductive tract, MV F56918, 90.6 mm ML, scale bar 5 mm, abbreviations as in Figure 6C.

Spermatophores: cement body clearly bipartite; aboral end elongate, cylindrical, connects to sperm reservoir via narrow duct which extends from nipple-like tip of cement body, connects to oral end by narrow neck (Figures 22B, 23); oral end shorter than aboral end of cement body, cylindrical, tapers evenly to terminal dilation; middle tunic commences along aboral part of cement body; ejaculatory apparatus coiled, extends into oral dilation of spermatophore. Spermatophores 4.8–6.0–8.5 mm long (SD, 1.5 mm), 0.25–0.30–0.50 mm wide (SD, 0.10); SpLI 8.4–10.6–12.6 (SD, 1.5), SpWI 3.18–5.28–9.43 (SD, 1.86).

Female reproductive tract: ovary hangs from dorsal wall of posterior viscero-pericardial coelom.

Oviduct thin-walled, continuous with body cavity; distally with thickened, glandular walls (oviducal glands). Nidamental glands, in mature animals, occupy large portion of ventral side of mantle cavity. Accessory nidamental glands anterior to nidamental glands (Figure 22C). Eggs spherical, 3.5–4.0–4.4 mm diameter (SD, 0.5); EgDI 4.0–4.3–4.6 (SD, 0.3).

Dorsal mantle with thick, cartilaginous subdermal layer; cartilaginous layer adheres closely to cuttlebone. Cuttlebone length approximately equal to mantle length; CbL males 47–55.9–65.6 (SD, 7.8), females 60.5–68.1–86.5 (SD, 9.7); outline oblong (Figure 24A,B); CbWI males 29.4–32.2–34.1 (SD, 1.7), females 28.7–31.9–33.7 (SD, 1.8); acuminate,

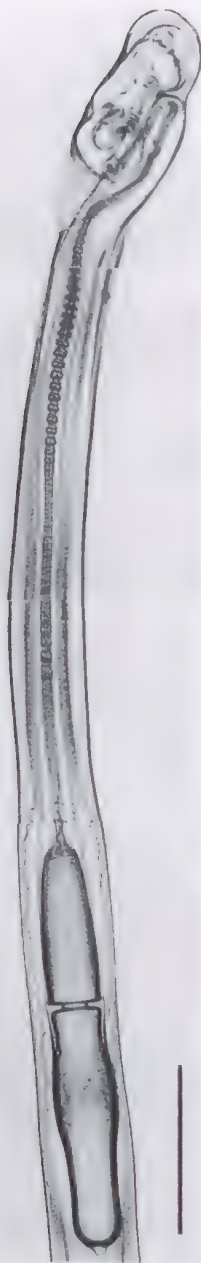


Figure 23 *Sepia sulcata* Hoyle; spermatophore, oral end, MV F56919, 67.6 mm ML, scale bar 1 mm.

acute anteriorly; acuminate, acute posteriorly (pointed). Dorsal surface yellowish; flat medially, curved, convex laterally; texture smooth, not pustulose. Dorsal median rib present; distinct; broadens anteriorly; lateral ribs present, distinct. Chitin present over entire surface of cuttlebone, with thicker band on each side. Spine present; short; SLI males 2.5–3.3–4.4 (SD, 0.8), females 1.2–

2.9–3.5 (SD, 0.8); curves dorsally; keel(s) absent; cuttlebone smooth between spine and outer cone; ventral notch at base of spine absent. Dorsoposterior end of cuttlebone with short, median longitudinal ridge anterior to, and separate from spine (Figure 24A). Striated zone convex (slightly); StZI males 60–63.5–67.8 (SD, 2.8), females 57–64–71.3 (SD, 5.1). Last locus flat; LoLI males 28.9–35.0–40.3 (SD, 3.9), females 25–33.7–39.2 (SD, 6.1); one-third length of striated zone (approximately); LoL/StZ(%) males 44.0–55.4–67.2 (SD, 8.4), females 35–53.5–66.5 (SD, 13.1). Sulcus extends along entire length of bone; shallow, narrow; flanked by rounded ribs bordered laterally by shallow grooves (distinctive). Anterior striae inverted U-shape (slightly wavy due to ribs). Limbs of inner cone extend anteriorly to end of striated zone. Inner cone limbs broaden posteriorly, raised to form ledge; ledge flat, not thickened (Figures 24B, 25). Outer cone chitinous, not calcified; narrow throughout; lateral limbs not flared ventrolaterally; outer cone strongly recurved ventral to spine, forms cup-like structure.

Body papillae present; dorsal mantle with longitudinal row of up to 10 short longitudinal ridges along each side close to fins (not visible in all specimens examined); ventral mantle with longitudinal row of 6 narrow ridges along each side close to fins; anterior-most pair and posterior 2 pairs shorter than rest (Figure 18C) (short ridges sometimes difficult to detect in small specimens). Head and arm papillae absent. Colour (alcohol preserved specimens): Head pale, without colour pattern. Dorsal mantle pale buff pinkish-brown; paired dorsal eye spots absent. Fins pale; without markings at base. Arms without markings. Ventral pigment absent. Dorsal and ventral longitudinal ridges pinkish-orange.

Original reference

Hoyle, W.E. (1885). Diagnoses of new species of cephalopoda collected during the cruise of H.M.S. "Challenger." Part II. The Decapoda. *Annales and Magazine of Natural History* (5) 110: 181–203.

Type locality

Indonesia: Arafura Sea, off Ki Is., 5°49'15"S 132°14'15"E; 255 m.

TYPE: Holotype, BMNH 89.4.24.77, male, 53.2 mm ML.

Distribution

Indonesia, Arafura Sea, off Ki Is., 5°49'15"S 132°14'15"E to Australia: Western Australia, North West Shelf, 19°58'S 115°13'E; depth range 404–150 m. Habitat mud (holotype blue mud), silt, rock.

Remarks

This species previously was known only from the

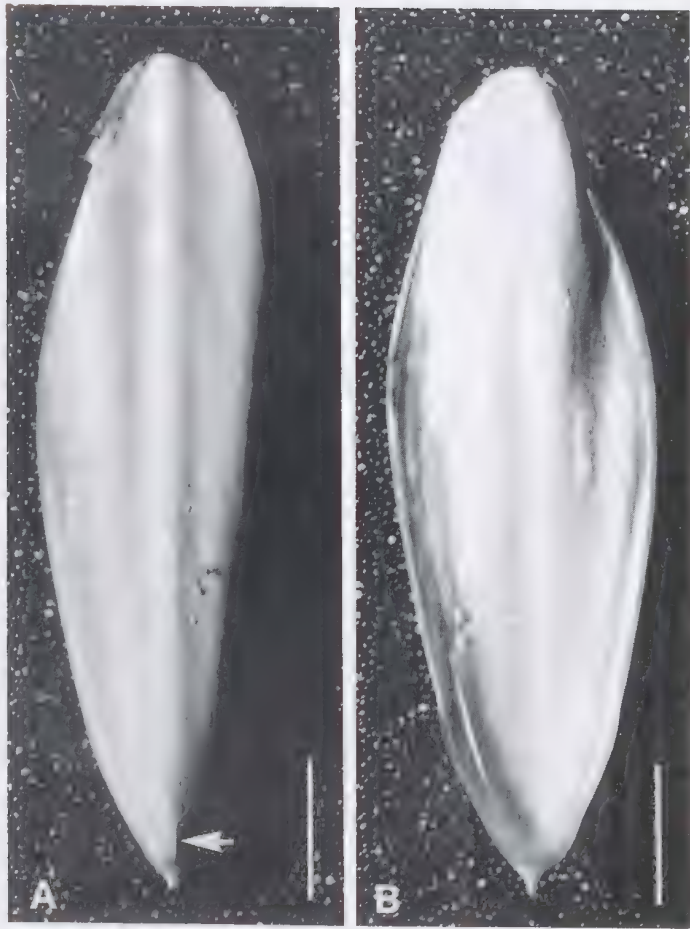


Figure 24 A-B, *Sepia sulcata* Hoyle; A, cuttlebone, dorsal view, female WAM 339-86, 60.9 mm ML, arrow indicates median longitudinal ridge; B, ventral view, same specimen. Scale bars 6 mm.

type specimen. The discovery of new material among collections of the Western Australian Museum and Museum of Victoria has enabled a redescription based on the type and this new material, thus adding information on females (which previously were unknown) and has provided more information on the distribution of the species. In most respects, the Australian material conforms to Hoyle's (1885) original description which was based on the single male type specimen. Some differences, however, were found. The two dorsal arms are described as bearing biserial suckers. We have found that while suckers are biserial for most of the length of these arms, they are arranged in 4 series on the extreme distal tips of both arms in males. The club suckers in the type specimen are arranged in 7 rows, while those of the Australian specimens are usually in 5 rows, rarely 6, or 7. Hoyle (1885) reports the presence of a few minute papillae on the postero-

dorsal surface of the mantle. Aside from the short bars described above (which may be the same as those that Hoyle (1885) is referring to), no other papillae could be found on the dorsal side of the mantle in the specimens examined in this study. The modification of the hectocotyliised arm in the type specimen is typical of immature males of this species. While the suckers are reduced on the left ventral arms in all males, the degree of development of the median furrow differs depending upon the state of maturity of the animal. In males determined to be immature due to the absence of spermatophores in the spermatophore storage sac, the median furrow on the hectocotylus may be absent (as in the type specimen (Figure 20A)), or only weakly developed as a small pit, or depression at the base of the arm. In mature males, the furrow is deep and pronounced (Figure 20B). Hoyle (1885) describes the suckers on the distal portion of the

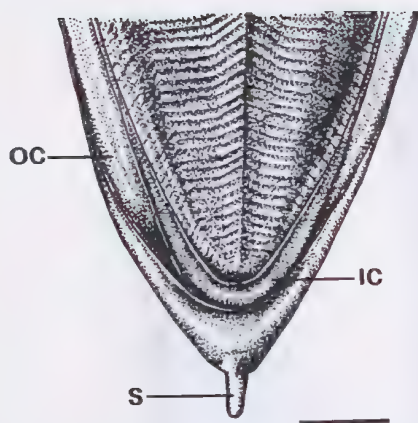


Figure 25 *Sepia sulcata* Hoyle; posterior end of cuttlebone, ventral view, female WAM 343-86, 65.1 mm ML, scale bar 4 mm, (IC – inner cone; OC – outer cone; S – spine).

hectocotylied arm as biserial, but in all material examined in this study, these suckers are tetraserially arranged. The depth range occupied by this species is broad (404–150 m). There is some evidence to suggest that there might be a migration into relatively shallower waters for spawning. The largest males (65.9–67.6 mm ML), and females (85.7–96.2 mm ML) were collected at depths between 184–150 m (MV 56918, MV 56919, WAM 3100–83), and all mature, while those collected at depths in excess of this range are smaller and include immature animals.

This cuttlebone of this species shows some similarities with that of *S. australis* Quoy and Gaimard, 1832 from South Africa. In both species, the cuttlebone is narrow and oblong, distinctly pointed anteriorly, with pronounced dorsal median and lateral ribs and, on the ventral side, the lateral ribs in both species are bordered by grooves. The ventral grooves, and sulcus are much deeper and more pronounced in *S. australis* than in *S. sulcata*. Both species have the short, median ridge on the dorsal side of the cuttlebone, anterior to the spine. The posterior end of the cuttlebone is broader in *S. sulcata*; in *S. australis* outer cone is poorly developed and the inner cone is not raised forming a ledge. *S. australis* is darkly pigmented, unlike *S. sulcata* and has a distinctive unbroken longitudinal ridge at the base of the fins. The arm suckers in *S. australis* are arranged in four series, unlike those seen in this species.

DISCUSSION

With the inclusion of *Sepia plana*, *S. senta* and *S. sulcata*, 29 nominal sepiids are now known to occur in the Australian fishing zone (200 nautical miles

from the coast). In addition to the three species described above, the following sepiids are found off northwestern Australia: *Metasepia pfefferi* (Hoyle, 1885); *Sepia cottoni* Adam, 1979; *S. elliptica* Hoyle, 1885; *S. irvingi* Meyer, 1909; *S. latimanus* Quoy and Gaimard, 1832; *S. opipara* (Iredale, 1926); *S. papuensis* Hoyle 1885; *S. pharaonis* Ehrenberg, 1831; *S. smithi* Hoyle, 1885, and *Sepiella weberi* Adam, 1939. These latter species (with the exception of *S. irvingi*) are widely distributed in the Northern Australian Region, a zoogeographic zone recognised by Wilson and Allen (1987). This zone extends across northern Australia to southern Queensland. Though regions of overlap occur on each side of the continent, the predominantly tropical Northern Australian assemblage largely differs in species composition from the more temperate Southern Australian fauna. Most marine species within this region also occur elsewhere in the Indo-West Pacific, though many Australian endemics are found in the zone. Among the sepiids, *S. cottoni*, *S. irvingi*, *S. opipara*, *S. plana*, *S. smithi*, *S. senta* and *M. pfefferi* are known only from Australia at present. The presence of an animal very similar in appearance to *S. senta* in the Philippines, either a distinct species, or population, suggests that *S. senta* is unlikely to be a true Australian endemic. *Sepia irvingi* is classed by Lu (in press, a) as belonging to the Western Overlap zone. It is included in the list of species above as its distribution extends to the North West Shelf.

Species in the genus *Sepia* are easily distinguished from the two other sepiid genera, *Sepiella* and *Metasepia*. *Sepiella* differ from other sepiids by the presence of a gland, and gland pore at the posterior end of the mantle between the fins, the mantle cartilage has a triangular tubercle, and the sepium has very short limbs. *Metasepia* can readily be recognised by the distinctive rhomboidal sepium which is situated in the anterior 2/3 – 3/4 of the mantle (Khromov *et al.*, in press). Table 10 lists some characters which can be used distinguish representatives of the genus *Sepia* found off northwestern Australia.

ACKNOWLEDGEMENTS

We thank F. Naggs (BMNH), S. Slack-Smith (WAM) and V. Wadley (CSIRO) for providing specimens. For help with scanning electron microscopy we are grateful to F. Brink and D. Vowles at the E.M. Unit, Research School of Biological Sciences, Australian National University (ANU). Thanks also to M. Norman (Melbourne University), C. Rowley (Museum of Victoria) and J. Wilson (ANU) for assistance with photography and to A. Gibbs for providing work space and facilities at the Research School of Biological Sciences in Canberra (ANU) to Amanda Reid. This

work was made possible by a support grant from the Australian Biological Resources Study Program to C.C. Lu. Thanks finally to the reviewers whose comments greatly improved this manuscript.

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Manuscript received 2 October 1996; accepted 29 April 1997.

A new cranioid brachiopod from the Eocene of southwest Australia

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Abstract – *Westralicrania zenobiae* sp. nov. is described from the Late Eocene Nanarup Limestone in the Bremer Basin of southwest Australia. The genus *Westralicrania* is shown to be a valid taxon, and a revised diagnosis is presented. This is the first record of the genus from the Eocene.

INTRODUCTION

The Nanarup Limestone Member of the Werillup Formation is a yellow and white bryozoan calcarenite that reaches up to 5 m in thickness. The most extensive outcrop is in the Nanarup Lime Quarry, 19 km east of Albany, Western Australia. The Nanarup Limestone has a rich, largely undescribed fauna, dominated by bryozoans and consists, in addition to brachiopods, of foraminifers, echinoids, asteroids, crinoids, sponges, bivalves, gastropods, nautiloids, crabs and shark teeth. Beside the cranioid brachiopod described below, there are some eight different articulated brachiopods of the order Terebratulida present in the unit which are currently being studied.

The fauna of the Nanarup Limestone indicates a Late Eocene age, containing foraminifers belonging to the "Tortachilla Microfaunule" (McTavish 1966). This age is supported by the brachiopod fauna, which includes three species described from the Tortachilla Limestone in South Australia (Allan 1940, Thomson 1927). These are *Stethothyris pectoralis*, *Aldingia furculifera* and *Gryphus labiatus*. Furthermore, McNamara and Philip (1980) recorded the echinoid *Echinolampas posterocrassa* from the Nanarup Limestone. This species is also present in the Tortachilla Limestone. McGowran's examination of the planktonic foraminiferal assemblage indicates that the Nanarup Limestone Member is definitely part of the Tortachilla horizon and correlates with the foraminiferal highest Zone P14 and low Zone P15 (McGowran, 1989).

All of the specimens of the *Westralicrania* species examined and described below are housed in the Western Australian Museum (WAM) collection. The following measurements were made of the inside of the ventral valve (Figure 1); maximum valve length (L1), length from posterior margin to anterior of median septum (L2), length from posterior margin of limbus to anterior of median septum (L3), length of posterior muscle scar (L4),

length of median septum (L5), maximum valve width (W1), width from inside limbus to median septum (W2), width of lateral limbus (W3). The length of the exterior flattened attachment area (L6) and the width of the exterior flattened attachment area (W4) were also measured.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Dumeril, 1806

Subphylum CRANIIFORMEA Popov, Bassett,
Holmer and Laurie, 1993

Class CRANIATA Williams, Carlson, Brunton,
Holmer and Popov, 1996

Order CRANIIDA Waagen, 1885

Superfamily CRANIDIDEA Menke, 1828

Family CRANIIDAE Menke, 1828

Genus WESTRALICRANIA Cockbain, 1966

Revised diagnosis

Exterior of shell pustulose to spinose; ventral valve interior densely endopunctate. Posterior muscle scars on slightly raised platforms, anterior muscle scars in shallow pits.

Remarks

Lee and Brunton (1986) placed *Westralicrania allani* Cockbain, 1966 in the genus *Danocrania* because of the pustulose nature of the exterior and the apparent tuberculate interior. Neither the type material of *Westralicrania allani*, originally described from the Pirie Calcarene (now referred to as part of the Cardabia Formation of Middle Paleocene age [Hocking *et al.* 1987]), Denham, Peron Peninsula, Shark Bay, of Western Australia, nor the new species herein described from the Nanarup Limestone in southwest Australia, fit the generic diagnosis of *Danocrania*. This is because the

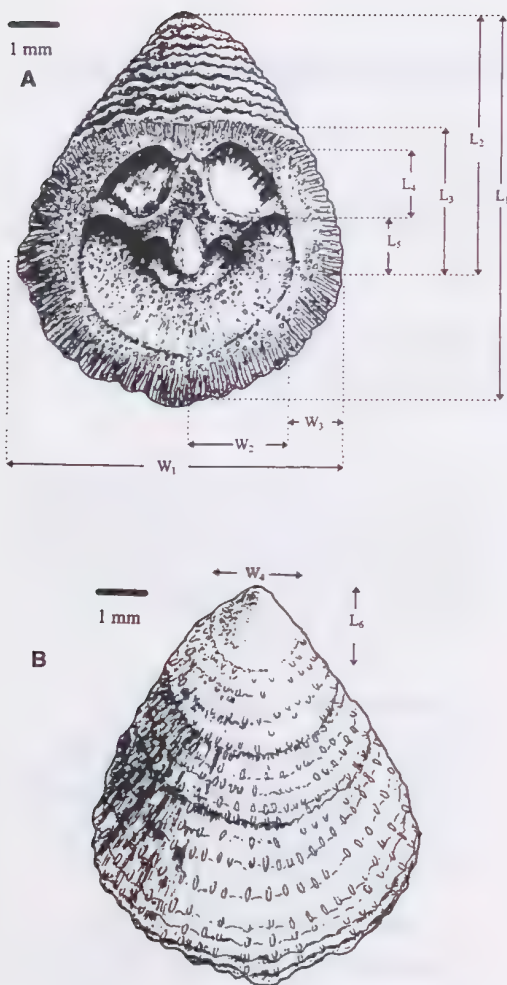


Figure 1 A, Sketch of ventral valve interior and measurement parameters of *Westralicrania zenobiae*: L_1 , maximum valve length; L_2 , length from posterior margin to anterior of median septum; L_3 , length from posterior margin of limbus to anterior of median septum; L_4 , length of posterior muscle scar; L_5 , length of median septum; W_1 , maximum valve width; W_2 , width from inside limbus to median septum; W_3 , width of lateral limbus. B, Sketch of ventral valve exterior and measurement parameters of *Westralicrania zenobiae*: L_6 , length of exterior flattened attachment area; W_4 , width of exterior flattened attachment area.

posterior muscle scars in *Westralicrania* are raised on platforms and without pits. In *Danocrania* the muscle scars occur in pits and not on platforms. *Westralicrania* is therefore regarded as a valid genus.

Westralicrania zenobiae sp. nov.

Figures 1,2

Diagnosis

Relatively large species of *Westralicrania*. Exterior valve with radiating short spines arranged in lines. Interior posterior muscle scars large; median septum short; pseudointerarea large and anacline.

Etymology

The species is named in honour of my wife, Zenobia. In Greek, Zenobia means "her father's jewel".

Material examined

Holotype WAM 94.29, ventral valve from the Nanarup Limestone (Late Eocene), Nanarup Lime Quarry. Paratypes WAM 94.30 to 94.40, ventral valves from the same horizon and locality as the holotype.

Other material

WAM 94.41, a ventral valve from the Nanarup Limestone, near Manypeaks Homestead. WAM 94.28 and WAM 88.373, dorsal valves from the Toolinna Limestone, Israelite Bay.

Description

Ventral valve

Shell reaches a maximum known length of 11.7 mm (Table 1); triangular to pear shaped (Figure 2A-I), width 80% of shell length (SL); dorso-ventrally flattened. Growth lines on exterior indicate mixoperipheral growth, pronounced growth lines on the pseudointerarea. Exterior has elongated pustules to spines which radiate in lines from the posterior attachment area behind the pseudointerarea with some intercalation (3 per mm). The spines themselves point in a posterior to anterior direction. Attachment area is a distinct elliptical region of flattening (16% SL, 22% shell width [SW]). Because pseudointerarea is slightly anacline, shell is raised from attachment area. The triangular pseudointerarea (31% SL) bears definite stepped growth lines, 3 in the smallest to 11 in the largest. A flat limbus entirely surrounds concave depression of shell interior. Posteromedian extension of limbus impinges slightly on depression before it drops to a shallow depression between large paired, raised muscle scars (20% SL). Traced anteriorly, this depression leads to a small median septum or ridge (13% SL) with raised anterior muscle scars on each side with single depression in each. Interior of shell is endopunctate, which in the smallest specimen, leads to shell appearing as if it is tuberculate. Endopunctae radiate from posterior margin in front of pseudointerarea. Limbus and posterior

margin similarly endopunctate, some of the punctae forming linear depressions perpendicular to shell edge.

Dorsal valve

Dorsal valve (WAM 94.28) subcircular (Figure 2J–L). Exterior surface has a number of growth lines with radiating spines (3 per mm). Valve slightly conical in shape, top of cone 0.25 to 0.3 distance from posterior margin. Interior has pronounced limbus slightly angled to interior curvature, beginning at posterior-lateral margin; extends around the shell. Towards anterior of shell it widens, being widest at anterior margin. Shell concave, greatest depth at cone top near posterior. Posterior muscle scars are slightly raised from the wall and parallel to it. Anterior muscle scars on the base of shell, triangular in shape. Anterior to these scars is a median ridge which extends 0.3 diameter of the valve with two large depressions either side. Shell endopunctate throughout, endopunctae radiating in a linear fashion.

Intraspecific variation

The larger the specimen, the greater the number of growth lines in the pseudointerarea, each line becoming more densely spaced as the shell gets larger. Furthermore, the greater the shell size the greater the number of radiating lines of spines on the exterior surface of the shell. WAM 94.34 has interior ridge anterior to the median septum from the anterior muscle scars to the margin in an anterior lateral direction. The shell is slightly

convex. Other specimens do not show these features. WAM 94.36 and WAM 94.37 are markedly depressed anterior to the median septum and anterior muscle scars. There is a ridge present, dividing area into two equal sized pits. This is not observable in WAM 94.29 and WAM 94.34 nor, due to wear, is it apparent in WAM 94.30–33. WAM 94.35, WAM 94.38 and WAM 94.40,41 have a wider ridge or “bridge” between the anterior muscle scars and limbus than other specimens (Figure 2G). WAM 94.37 shows clearly the endopunctae in lines radiating from the pseudointerarea margin. These lines change direction on the limbus to become perpendicular with the shell edge. In WAM 94.38 the pseudointerarea is less pronounced than in other specimens. Around the endopunctate limbus an anterior margin, stemming from the first growth line of the pseudointerarea, surrounds the shell. This is also present in WAM 94.40 and WAM 94.41. The margin is smooth, flat and not punctate. It is possible that such a margin was present on the other specimens but was worn away. WAM 94.39 (Figure 2H,I) is appreciably smaller than the other specimens. It is flatter internally, lacking distinctive muscle scars. The endopunctae produce numerous raised areas which appear as tubercles. The middle of the three growth lines in the pseudointerarea has two flat spines pointing posteriorly. The “roughness” of the edges of growth lines in other specimens may indicate that they too possessed such spines at some stage.

Table 1 Measurements of *Westralicrania zenobiae* ventral valve dimensions as indicated in figure 1 (all measurements in millimetres).

Specimen	Length 1	Length 2	Length 3	Length 4	Length 5	Length 6	Width 1	Width 2	Width 3	Width 4	G. Lines	S.Lines
WAM 94.29	8.6	6.0	3.3	1.7	1.1	1.4	7.0	2.5	1.2	1.6	9	36
WAM 94.30	7.9	4.9	3.2	1.5	0.9	–	7.0	2.4	0.9	–	6	29
WAM 94.31	10.3	6.5	4.0	1.9	1.0	1.5	8.6	3.0	1.2	1.8	–	36
WAM 94.32	11.7	–	–	–	–	2.1	8.5	–	–	2.1	–	28
WAM 94.33	7.7	4.9	3.5	1.6	1.0	1.9	6.7	2.3	1.0	2.3	–	27
WAM 94.34	9.1	6.1	3.9	1.7	1.0	1.5	7.9	2.7	1.2	1.7	11	35
WAM 94.35	7.8	4.9	3.6	1.6	1.0	1.0	6.8	2.1	1.0	1.6	11	28
WAM 94.36	9.1	6.0	4.5	1.8	1.1	1.5	8.0	2.9	1.2	1.7	–	26
WAM 94.37	9.5	6.9	–	1.7	1.4	1.6	7.4	2.5	1.3	2.1	–	37
WAM 94.38	8.7	5.6	4.3	2.1	0.9	1.5	7.7	2.7	1.2	1.9	–	–
WAM 94.39	4.8	3.3	2.2	0.9	0.6	1.3	3.8	1.0	0.8	1.7	3	26
WAM 94.40	8.5	6.3	3.7	–	1.1	2.2	6.6	2.5	1.0	2.4	–	–
WAM 94.41	9.6	6.5	4.0	1.7	0.9	–	7.3	2.5	0.9	–	9	29
AVERAGE	8.7	5.7	3.6	1.7	1.0	1.6	7.2	2.4	1.1	1.9	N.A	30

NB: G. Lines indicate growth lines and S. Lines indicate ribs on exterior of the shell.

Dorsal valve measurements:

SPECIMEN	LENGTH	WIDTH	DEPTH
WAM 94.28	7.3	7.8	2.1
WAM 88.373	7.0	7.8	2.1

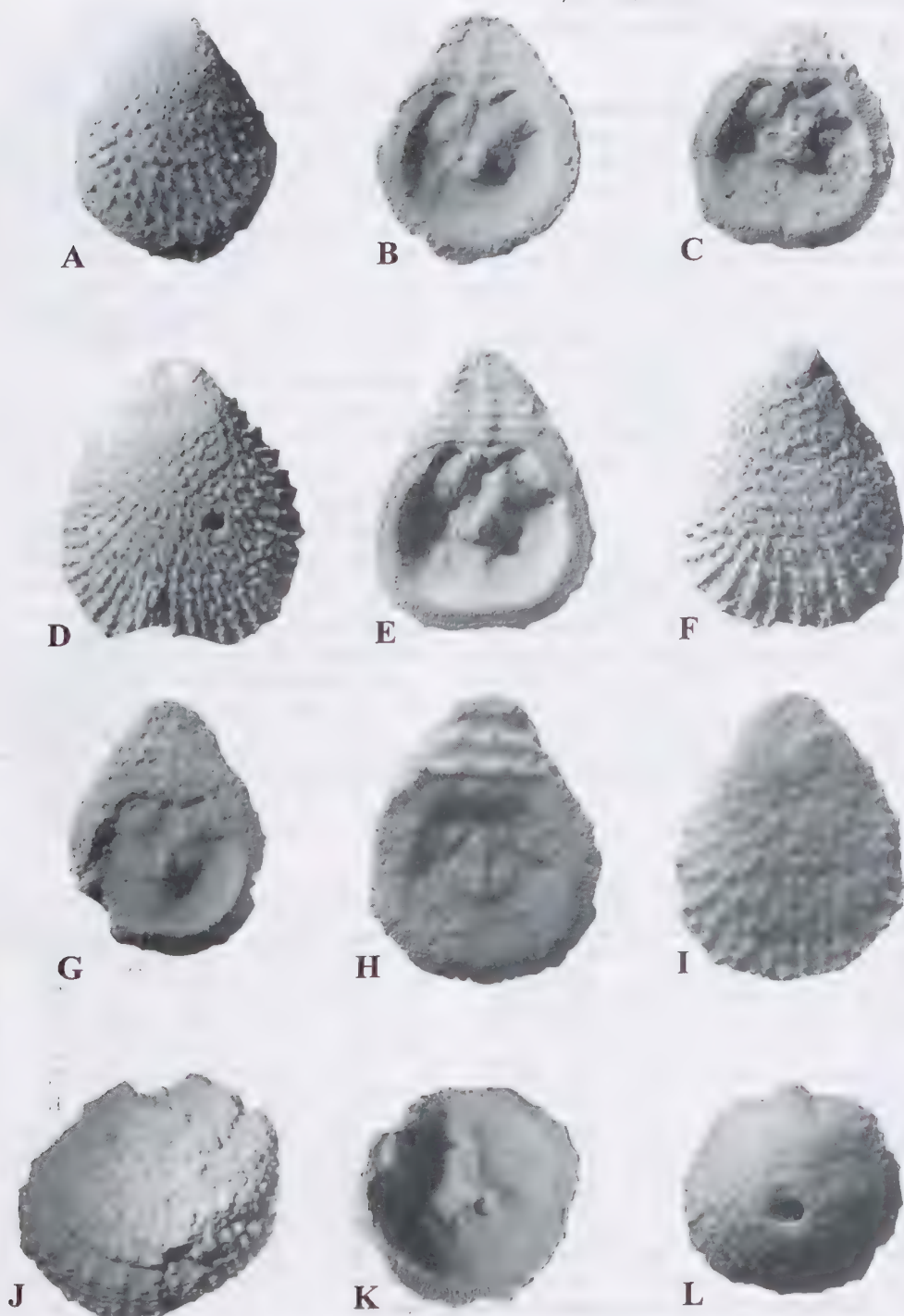


Figure 2 *Westralicrania zenobiae*. **A:** WAM 94.29, Holotype, ventral valve exterior x 5; **B:** WAM 94.29, Holotype, ventral valve interior x 5; **C:** WAM 94.30, Paratype, ventral valve interior x 5; **D:** WAM 94.31, Paratype, ventral valve exterior x 5; **E:** WAM 94.41, Paratype, ventral valve interior x 5; **F:** WAM 94.41, Paratype, ventral valve exterior x 5; **G:** WAM 94.40, Paratype, ventral valve interior x 5; **H:** WAM 94.39 (Juvenile), Paratype, ventral valve exterior x 10; **I:** WAM 94.39 (Juvenile), Paratype, ventral valve interior x 5; **J:** WAM 94.28, dorsal valve exterior x 5; **K:** WAM 88.373, dorsal valve interior x 5; **L:** WAM 88.373, dorsal valve exterior x 5.

Remarks

In overall size *Westralicrania zenobiae* is generally larger than *Westralicrania allani* (4.8–11.7 mm for *W. zenobiae* compared with 2.2–6.8 mm for *W. allani*). The posterior muscle scars are comparatively larger (20% : 12.5% of total valve width), whereas the median septum is comparatively shorter in *W. zenobiae* than *W. allani* (11.1% : 28.6% of total valve length). There are significantly more growth lines in the pseudointerarea of *W. zenobiae* than in *W. allani* as it is comparatively longer. The spines on the exterior surface of *W. zenobiae* are relatively shorter on *W. zenobiae*, but they radiate in lines whilst those on *W. allani* have no apparent regularity. The pseudointerarea is anacline in *W. zenobiae* and apsacline in *W. allani*.

W. allani was originally described from Shark Bay (Cockbain 1966). Nine further specimens of *W. allani* (WAM 84.579[x4], 84.580 – 84.583, 92.714) have been collected from the Cardabia Calcarene, Giralia Range, Carnarvon Basin, Western Australia of Middle Paleocene age. They accord well with the description of the species by Cockbain (1966). The size range of the specimens is slightly larger (6.31–8.76 mm) than those from Shark Bay.

ACKNOWLEDGEMENTS

I would like to thank Dr J. Backhouse for the use of the type specimens of *Westralicrania allani* from the Geological Survey collection, Ms K. Brimmell for photographing the specimens of *Westralicrania zenobiae* and my wife Zenobia for the camera lucida diagram of the ventral shell. Special thanks must go to Dr K. J. McNamara for all his assistance, advice and support in preparing this paper.

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Manuscript received 14 February 1997; accepted 4 June 1997.

An engraved slate fragment from Walyunga, Western Australia

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Abstract – A small engraved fragment of slate from an archaeological site near Perth is analysed by intensive microscopic examination and through replication experiments. Various types of markings are present on both faces of the plaque. These intentionally made incisions are identified and distinguished from the numerous taphonomic marks also present. The anthropic markings are described in terms of their production processes, including the sequence in which they were made, and the directions from which they were drawn, almost certainly by a steel tool. It is concluded that the object was engraved on both sides before it was fractured and then worn by sediment. One side bore a very small structured arrangement that may have been iconic, the other a rectangular grid pattern. Both were engraved with a steel point, and possibly with the same tool.

INTRODUCTION

Walyunga is an archaeological open-air camp site, located in the Walyunga National Park, near the west bank of the Swan River and 38 km north-east of Perth. It is marked by a large surface scatter of stone tools on the deflated surface of a quartz sand dune and has been examined on various occasions (Butler 1958; Akerman 1969; Turner 1969; Pearce 1978).

Excavation at the site revealed a vertical distribution of occupation evidence to at least 1.4 m or 1.8 m, at which depth a charcoal sample produced a radiocarbon age in the order of 8000 years. This is in agreement with four other carbon dates from further up in the stratigraphy, which are all in proper sequence relative to depth (Pearce 1978, Table 1). The lithics include scrapers, adze flakes and 'fabricators', 'flat adzes', geometric microliths and asymmetric backed points. The latter two types were limited to levels above c. 3200 years BP, the 'flat adzes' to above c. 4500 BP. The prolific artefact assemblage is also characterised by typical tula slugs (cf. Bednarik 1977, Fig. 2). In addition there is a component of larger tools.

A distinctive change in tool material occurs at 4500 BP: before then, chert and silcrete are preferred, but after that time mylonite is used almost exclusively. Since this latter material has inferior flaking characteristics, it has been suggested that the earlier coastal stone sources became unavailable, perhaps by a rising sea level (Pearce 1978). A similar pattern has been observed at other archaeological sites in the region, leading to the assumption that Eocene chert sources now below sea level were inundated by about 6000 BP

(Glover 1979, 1984; Glover *et al.* 1979, 41; Glover *et al.* 1993).

In the surface deposit of the site, numbers of artefacts made from European glass and porcelain have been observed, as is also the case at other post-contact sites in the area, such as Orange Grove (Dodds *et al.* 1991) and Bullsbrook (C. Dortch, pers. comm.). Among the remains at Walyunga, W. H. Butler collected a small plaque of slate with incised markings in July 1958. It is catalogued in the anthropology collection of the Western Australian Museum and marked number A12748. This surface find appears to be a fragment of a roofing tile, as indicated by one straight and artificially bevelled edge. Mr C. Dortch and Mr P. Bindon of the Western Australian Museum suggest that the slate derives from the British Isles, perhaps Wales, and was imported in the 19th century. Mr Bindon has established that there was a cottage at the site in the last century, but he has also pointed out (P. Bindon, pers. comm.) that writing slates may bear a bevelled edge in the wooden frame. Remains of a shepherd's hut were still observed near the Walyunga site in the 1950s (G. Kendrick, pers. comm.). The occurrence of marine-derived calcarenite material in the lithic assemblage at Walyunga (G. Kendrick, pers. comm.) suggests that this site may have a recent sedimentary history similar to that of Orange Grove, where such material is thought to have arrived with guano fertiliser (Dodds *et al.* 1991).

The markings on the Walyunga slate fragment had not previously been examined in any detail. It was sent to me for study in mid-1996. The following report describes the incisions and various microscopic observations.



Figure 1 The engraved slate fragment from Walyunga.

GENERAL OBSERVATIONS

The slate fragment is 51.8 mm long, 31.9 mm wide (parallel to bevelled edge), and its thickness varies only from 2.9 mm to 3.0 mm (Figure 1). It is of dark grey to very dark grey colour (Munsell Color Charts 7.5YR 3.5/0). Its two principal surfaces are perfectly flat, and the concentration of most of the taphonomic markings on them suggests that the fragment has undergone a complex history of kinetic damage before attaining its present size and shape. It appears to have begun its life as a roofing tile, and it seems that it has lain on the ground for a length of time before the surviving

fracture surfaces became exposed to kinetic wear.

In its present shape it received some edge wear, suggesting that it was transported in or on the sandy sediment, and for a time it must have been buried, at least partially, in the sediment. This is indicated by a residue of sandy soil in a recess among the edge fractures. The light-brown sediment comprises 10–15% sorted quartz grains of 150–250 μm , mostly angular and often irregularly shaped. Some grains are moderately rounded and of frosted surface, colouration ranges from clear to reddish. Smaller quartz grains occur also occasionally, but the soil seems to be characterised by a component of medium to coarse quartz sand locally derived from the decomposition of a granite.

In the following description of the plaque's markings, side A (Figure 2) refers to the face that bears the number along the edge which is bevelled on the second face, side B (Figure 4). Left hand (l.h.) refers in both cases to the straight and bevelled edge, so that 'top' and 'bottom' refer to different edges in considering the two faces (i.e. as depicted in Figs 2 and 4).

Side A (Figure 2)

Minor red pigment traces occur locally, caused by rubbing against the surface without causing mechanical damage. Older and more recent depressions on the surface can readily be discerned by the presence of a whitish deposit in the older depressions. The fractures forming the r.h. (right hand), irregular edge are worn to a micro-wane of about 90 μm width, whereas the wane-width consistently averages approximately 180 μm on the

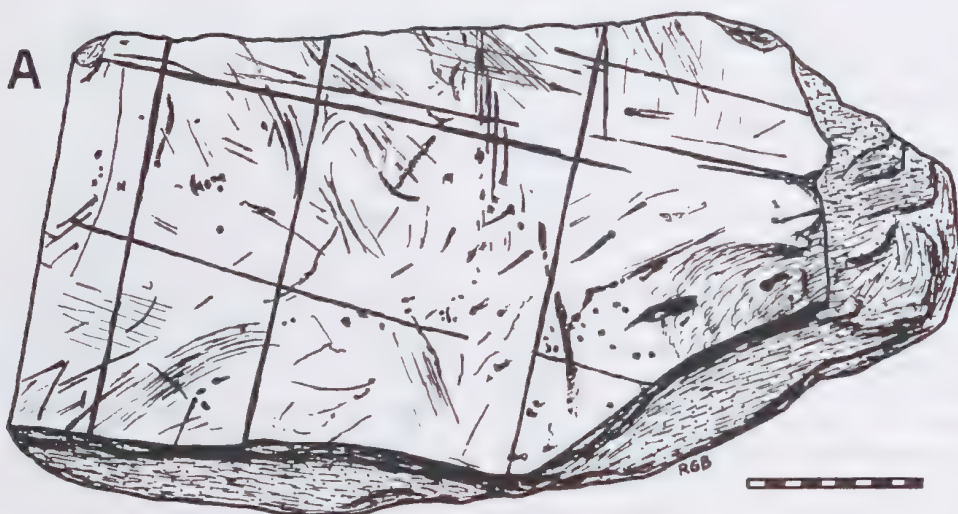


Figure 2 The markings on side A of the slate fragment. The scale is 10 mm long.

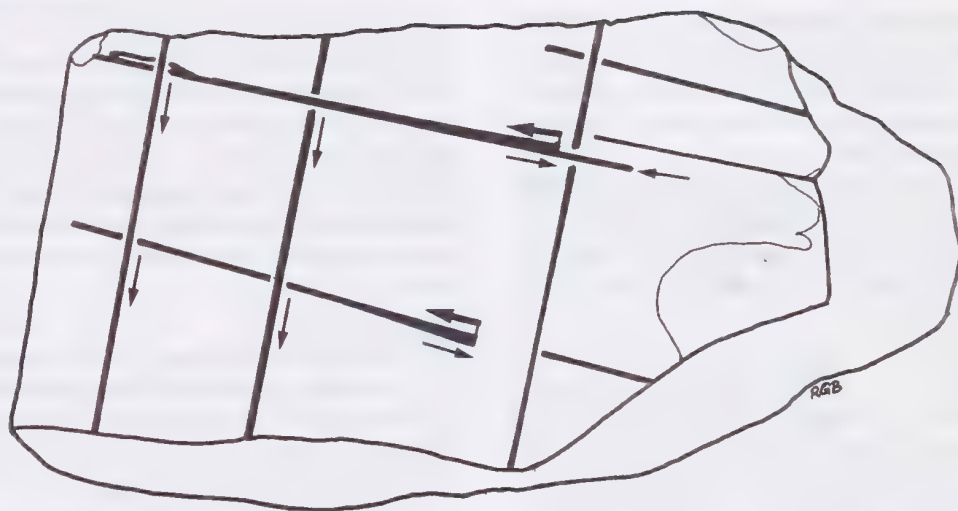


Figure 3 The marking sequence on side A, as determined by internal analysis.

top and l.h. edges and most of the bottom. The r.h. fractures can thus be considered to be considerably younger than the others which may well date from the time the object first came to be on the ground.

The surface of side A, especially the flat panel itself, bears innumerable taphonomic markings, including pitted impressions of quartz grains, 'comet-like' marks (pits with tail-like abrasive marks), and deeply gouged angular grooves with 'sculpted' cross-section. The marks are fully consistent with those made experimentally by angular quartz grains such as those described above from the local sediment. It appears that the object's flat surface rested against another hard flat surface, with quartz grains caught between and pressure applied as the object was moved a few millimetres. This would be consistent with the taphonomic action of trampling by humans or other animals, or it could have been caused when the object had been stacked with other slates. A prominent group of subparallel lines in the lower l.h. corner are not so readily explainable. They appear not to be intentional and postdate the engraved grid marks, as do practically all the major taphonomic markings.

The incised rectangular grid pattern has been drawn free hand, although its lines are almost rectilinear. The lines reach the edges in several places, and appear to predate all the fractures shaping the slate. They avoid the l.h. bevelled edge which they can be assumed to postdate. The three vertical lines are from 115 μm to 130 μm wide. The principal upper horizontal line is about 160 μm to 180 μm , ignoring effects of weathering, kinetic damage and diffuse groove edges. The lower horizontal line has a width of 140 μm to 165 μm .

The shorter horizontal lines in the r.h. upper area are thinner and less deep (100–125 μm and 110–120 μm respectively).

Of particular importance are the r.h. end of the lower principal horizontal line, and a distinctive change in depth in the upper line, roughly parallel to it but a little to the right. In my replication experiments on similar stone I was entirely unable to produce a similar groove morphology by any means other than the reversal (backing up on a line already drawn) of a steel point. In establishing the effects of various commonly used metal instruments that might reasonably have been available last century, I found that I could readily produce identical features with the point of a steel knife. I consider that it is impossible to replicate the precise morphology with any stone tool. Using a steel tool to engrave a line, the point of commencement always results in a sloping, concave commencement of the groove, and the groove floor bears a distinctive, 'compressed' appearance for at least the first 0.8 mm.

In past years I have conducted replication work with stone tools on various similar rock samples of low metamorphism (ranging from slate over phyllite to low-metamorphism schist). Narrow points even of broad chert flakes pressure-spalled, even when only slight pressure was applied, and would be quite incapable of producing more than a slight scratch on this surface without suffering damage. Quartz performs only marginally better. The production of a groove of 40 μm or 50 μm depth demands a certain minimum width of the point to prevent it from splintering. My experiments suggest that this minimum width of the groove is 350 μm . Such stone tool incision

marks made with wide enough points to withstand the pressure required to be applied always seem to have longitudinal striations, and they are often of non-symmetrical cross-section. For comparison, a steel sewing needle can produce a groove as narrow as 60 μm .

The engraved grid lines on the Walyunga specimen show no detectable variation in cross-section or width, no striations, and no marks suggesting any microspalling, all of which are typical features of stone point engravings on low-metamorphism rocks (Bednarik 1995a: 95–7). Stone points applied to such rock are sensitive to variations in pressure or speed of movement, as well as very minor variations in surface topography or stone hardness. Narrow points are prone to fracture along the course of a line, producing characteristic ‘jumps’. I have even observed variations in the distances of individual striations within a single groove drawn by just one tool application, and even when the operator did not notice any change in the precise tool orientation relative to the surface, or in the pressure applied. Nevertheless, the most reliable indication of a metal point occurs where a line changes direction, especially at points of sudden changes without lifting the tool from the surface. There are no changes in direction in the straight lines on the present specimen, but in view of the evidence in hand I have no hesitation attributing the intentional markings on side A to a metal tool, almost certainly a steel point.

This is strongly supported by the two reversal-marks already noted above. It is clear from this analysis that the upper of the two principal horizontal lines has been partly redrawn, which is also evident from the distinct bifurcation near its

l.h. end. The actual direction of most lines could be determined from several further observations: the morphology at crossings, where the second tool application tends to damage the corners of the off-side of the groove being crossed, and of course the second groove tends to be deeper at the crossing. Moreover, the two reversal-marks show the direction of the last tool applications in those cases. These tell-tales of tool direction agree consistently, and provide the marking sequence as depicted in Figure 3.

Side B (Figure 4)

An accumulation of densely packed, subparallel incisions larger than the one of side A occurs in the l.h. half of side B. Its markings are consistent with having been caused by a to and fro movement, with several sand grains caught between this and another flat surface and while considerable pressure was applied to these grains. This is suggested by locally quite deep gouges where angular grains can be seen to have been dragged.

In the lower design, a truncated circular line, we have the opportunity to observe the effects of directional change in tool application on the morphology of the groove. The outline is not well rounded, showing the kind of uneven change of direction that is typical for engravings on stone surfaces (Bednarik 1995b: 608; Marshack 1996). However, the groove width and groove profile remain uniform around the curvature, the latter being consistently between 120 μm – 150 μm .

The upper, more rectilinear figure has two particularly informative features, the corners marked in Figure 4. In these two instances, the direction of tool application changed abruptly. There is no interruption of the line at point (1), but

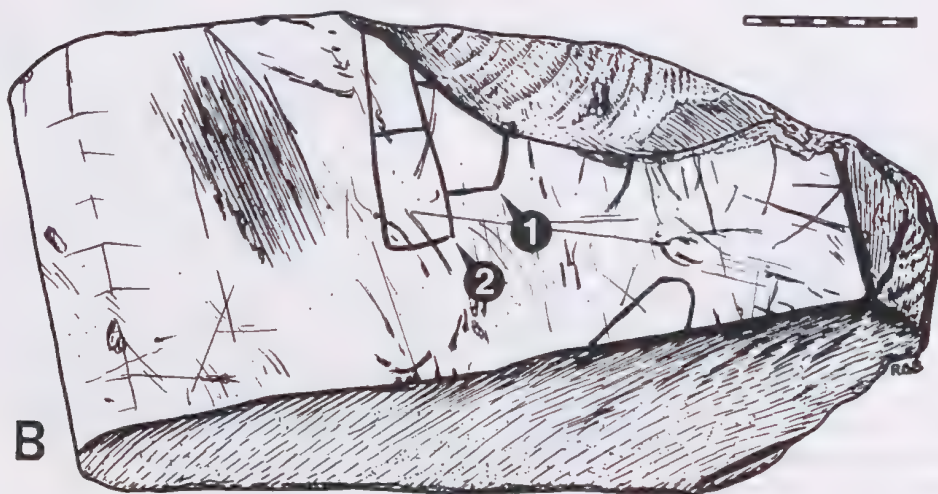


Figure 4 The markings on side B of the slate fragment. Scale 10 mm.

a telling change in width from the usual 120 μm – 150 μm to about 240 μm . At point (2), a distinctive gap of 90 μm occurs between the two lines which are both c. 150 μm wide. Since the same tool was almost certainly used in creating the whole design, the comparison of the two points shows that where the groove direction changed significantly without raising and turning the tool, the groove width changed, but not where the tool was lifted before continuing in a new direction. It is therefore suggested that the steel point was somewhat flattened, but was preferentially applied in the direction of its smaller width. This would imply the use of a knife point or similar instrument that permits the user good control over tool point orientation relative to direction of application.

Side B also bears numerous taphonomic marks, including on the fracture surfaces where they are most common along the outer edges. Some of the curved marks on the flat face may be tool made, but they are too faint and discontinuous to permit secure identification.

SUMMARY

This examination of the small engraved slate object from Walyunga suggests that it has a relatively long (in terms of the events documented on its surface being spread over many decades) and complex history. It is probably a fragment of a roofing tile, presumably imported from Britain during the 19th century. It was subsequently engraved with a steel point, possibly of a knife, on both sides. Neither the grid pattern on side A nor the motifs on the specimen's second face are typical of traditional Aboriginal graphic production. The designs on side B convey the impression that they may have formed part of a children's drawing, as their 'geometric' elements can be found in the work of juvenile artists. The grid pattern, however, reveals a steady hand and good control of the engraving tool, and is probably by an adult hand. One possible explanation would be that this pattern was part of a game board.

After its use as an engraving slate, the specimen was broken and its long taphonomic history began. This involved considerable mechanical wear through transport in or on a very abrasive sediment of irregular, often angular quartz grains. Trampling or rubbing against other hard surfaces occurred repeatedly, and more recently the object was buried in its final shape, at least partly, in the top of the sandy sediment.

It follows from this that it cannot be demonstrated that the artefact has been used by Aboriginal people, therefore its occurrence at the Walyunga occupation site may be fortuitous. One should not rule out the possibility, however, that the object has been used as a slate by Aboriginal

children during the nineteenth century. I have detected no evidence that would clarify this point.

ACKNOWLEDGEMENTS

My thanks are expressed to Mr Charles Dortch and the Western Australian Museum, for making this specimen available for detailed analysis. I also thank Mr Peter Bindon, Mr George Kendrick, Dr Patricia Vinnicombe and Mr Dortch for constructive comments on a draft of this paper.

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Sellnickiella (*Sellnickiella*) *biunguiculata* sp. nov.: a noteworthy species of Labidostomatidae from Australia (Acari: Actinedida: Labidostomatina)

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Abstract – *Sellnickiella* (*S.*) *biunguiculata* sp. nov. is described from Australia. This species shows an exceptional apomorphic character among Labidostomatidae: the lack of median unguis on legs II–IV. Otherwise, this species is a typical member of *Sellnickiella* (*Sellnickiella*), a gondwanan group which representatives recorded from South America, South Africa, Australia and New Zealand.

INTRODUCTION

The Australian labidostomid fauna was summarized by Atyeo and Crossley (1961a) who described two species of *Labidostoma*¹ Kramer which are now placed in *Sellnickiella* (*Sellnickiella*) Feider and Vasiliu, 1969 (Bertrand 1990a): *Sellnickiella* (*S.*) *womersleyi* (Atyeo and Crossley) and *S.* (*S.*) *adelaideae* (Womersley)². These authors (Atyeo and Crossley 1961b) also described some new species from New Zealand belonging to both *Sellnickiella* and *Labidostoma* (*Atyeonella*) (Feider and Vasiliu 1969; Bertrand 1990a). Others known species of *Sellnickiella* are restricted to southern hemisphere (Feider and Vasiliu 1970; Feider, Vasiliu and Calugar 1974; Bertrand 1990b; Bertrand and Theron 1992).

Although labidostomids are worldwide in distribution, they show biogeographic patterns at the generic or infrageneric level which allow us to consider them as good indicators of past relationships between continents. The homogeneity of the characters as their originality justify the fact that they constitute the suborder Labidostomatina (= Labidostomina) amongst the heterogeneous order Actinedida with a small number of valid genera (only four). Collections from the southern continents are still scarce, and increased knowledge is leading to a constant improvement of

traditional classification patterns, mostly based on morphological characters of palearctic species. Grandjean (1942) stated that the division of the genus *Labidostoma* was untimely. However, 50 years after, new data have shown four main groups, each assigned generic status: *Eumicolina*, *Akrostoma*, *Sellnickiella* and *Labidostoma* (Bertrand 1990a). *Labidostoma* is worldwide in distribution, and *Sellnickiella* is restricted in southern hemisphere. Description of a new Australian species is a contribution towards our knowledge of the labidostomid fauna of the southern continents.

The specimens discussed below are all lodged in the Western Australian Museum, Perth (WAM) and are stored in alcohol. Three were dissected and cleared in lactic acid. The following abbreviations are used:

ap.m.: antiaxial cheliceral appendice
apo1, *apo2*, *apo3*, *apo4*, *apo sej.*: ventral apodemes 1 to 4 and sejugal apodeme
bo.a, *bo.p*: trichobothria, anterior and posterior
cha, *chb*: cheliceral setae
da, *db*, *dc*, *dd*, *de*: paired opisthosomatic setae of dorsal files
E: eye
FE: frontal eye
ga, *ge*, *gr*, *gm*: fundamental paired aspidosomal setae (except trichobothria)
la, *lb*, *lc*, *ld*, *le*: paired opisthosomatic setae of lateral files
ly: lateral lyrifissure of dorsal shield
LE: lateral eye
LL: adoral lateral lips
ma, *mb*: usual paired infracapitular setae
p: pores of the cuticle
P1, *P2*, *P3*: paraproctal setae
SL: superior lip (labrum)
tα, *tπ*, *ti*: antiaxial, paraxial, and inferior terminal teeth of fixed digit of chelicera
tr: tracheal trunk

¹ This generic name is either spelt *Labidostoma* or *Labidostomma* by various authors. Etymologically, the Greek root 'stoma' (for mouth) is correct. This term was used by Oudemans (1904) who named the family Labidostomidae correcting the error of Kramer (1879). According to the International Code of Zoological Nomenclature, the valid family group name is Labidostomatidae, although the first genus described was *Nicoletia* Canestrini and Fanzago, 1877, and the term Nicolettiellidae (Canestrini, 1891) has been used by several authors (see Steyskal, 1970).

² Feider and Vasiliu (1969) wrongly attributed *S.* '*wommersleyi*' to Womersley (1935).

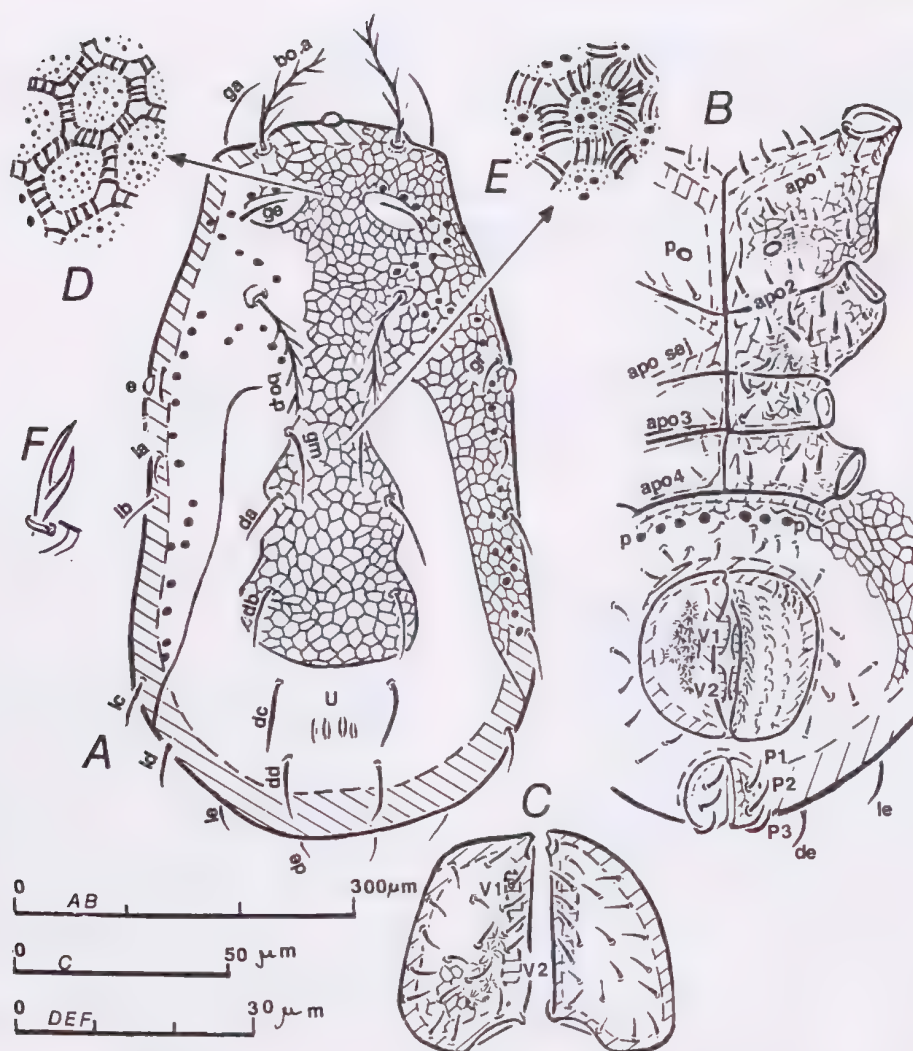


Figure 1 *Sellnickiella (Sellnickiella) biunguiculata* sp. nov.: A, dorsal shield female; B, ventral shield, male; C, progenital valves of female (nota: both valves are slightly separated in order to show their articulations at anterior and posterior extremities); D, E, cuticular reticular patterns of dorsal shield; F, famulus of tarsus I (dorsal).

*T*_ζ: terminal eupathidial seta of palp tarsus
U: U-shaped zone of dorsal shield
ω, *ω*₁, *ω*₂: solenidia of tarsus (palp or leg)

SYSTEMATICS

Genus *Sellnickiella* Feider and Vasiliu

Sellnickiella Feider and Vasiliu, 1969: 206.

Type species

Labidostoma brasiliense Sellnick, 1922, by original designation.

Remarks

This genus includes two subgenera: *Dicastricola*, which is only known from South America, and *Sellnickiella* which has been found on all the southern continents (Bertrand 1990a; Bertrand and Theron 1992); and *Sellnickiella*, which is noteworthy because unlike others members of the family it does not show uniformity of sclerification in adult stases and lacks a pair of "gland like organs" (which are subject to neotaxy in *Eunicolina*, and in some species of *Labidostoma*). The differentiated sclerification of the dorsal shield in *Sellnickiella* was well illustrated by Feider and Vasiliu (1970) and

may be related to immature sclerification (neoteny in the common sense of maintenance of pre-adult characters in adult stases). These characters are found in both subgenera, *Sellnickiella* and *Dicastricola*. The subgenus *Sellnickiella* also exhibits the peculiar morphology of the famulus (dorsal regressive seta of tarsus I), with two unequal branches which is unique among species of Labidostomidae. This morphology results from a regressive evolution with the complex primitive famulus being present in *Labidostoma* (Grandjean 1941).

Sellnickiella (Sellnickiella) biunguiculata sp. nov.

Material Examined

Holotype

♀, Dwellingup, Western Australia, Australia, 32°43'S, 116°04'E, 8 June 1978, pitfall traps, S.J. Curry (WAM 93/96).

Paratypes

Australia: Western Australia: 1 ♀, 1 ♂, Dwellingup, 32°43'S, 116°04'E, 8 June 1978, pitfall traps, S.J. Curry (WAM93/37–38); 4 ♂, 3 ♀, Mt Cooke, 32°25'S, 116°18'E, 27 April 1992, leaf litter, M.S. Harvey, J.M. Waldock (WAM 93/39–45).

Diagnosis

Sellnickiella (S.) biunguiculata is very similar to *S. (S.) womersleyi* (Atyeo and Crossley) from South

Australia, but can be distinguished by the bidactylous tarsi II–IV, the absence of lateral projections on the anterior edge of dorsal shield, the ornamental pattern of dorsal shield, and characters of the fixed digit of the chelicera, which is serrate and bears a strong blade.

Description

General Morphology (Figure 1)

Small elongated, long legged species, yellow to brown in alcohol. Leg I length similar to body length: dorsal shield ca. 600 to 650 µm, somewhat oval; chelicerae strong, ca. 150 µm in length; their strong digits come into view in dorsal examination before frontal extremity of dorsal shield beneath a small median eye (20 µm diameter). Dorsal shield (Figure 1A) bears usual pairs of setae with pairs *ga*, *gr*, *ge* *gm* and trichobothria *boa* and *bop* belonging to the aspidosoma, 1 ♂ lacks one pair, *ge*, as in *S. womersleyi* [see Atyeo and Crossley (1961)], dorsal and lateral files (*la*) to (*le*) and (*da*) to (*de*) on the opisthosoma.

Trichobothria long (more than 100 µm) with thin ciliation longer on anterior pair, which is inserted very close to anterior edge of dorsal shield. Distance between bases of anterior pair is 140 to 150 µm while in the posterior pair this distance is 160 to 180 µm. Anterior pair (*ga*) inserted ventrally. Cuticle regularly alveolated except in dorsal part behind level of lateral eyes where ornamentation is dissolved into a tiny punctated U-shaped area whose internal margins are limited by setae (*gm*)

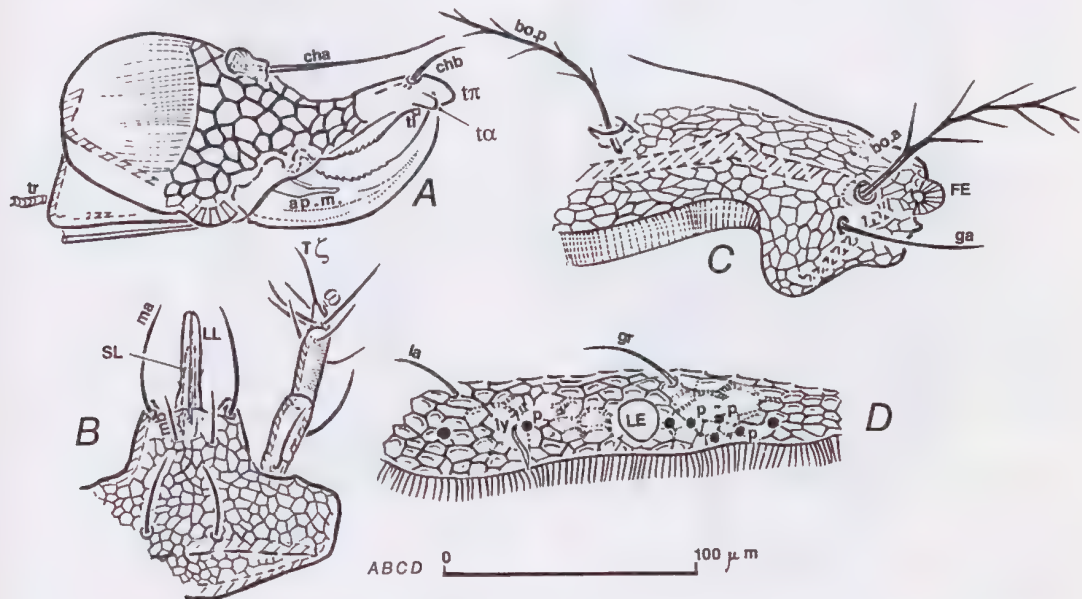


Figure 2 *Sellnickiella (Sellnickiella) biunguiculata* sp. nov: A, chelicera, antiaxial view; B, infracapitulum and palp, ventral view; C, anterior part of dorsal shield, lateral view; D, ocular zone of dorsal shield, lateral view.

and dorsal setae (*da*) and (*db*). Cuticle exhibits numerous pores mainly in two regions: interthoridic area and above lateral margin of dorsal shield in alveolated area.

Chelicera (Figure 2A)

Chelicerae are typical of the genus, and very similar to that of *S. womersleyi*, with a strong fixed digit bearing tiny inferior teeth. Fixed and mobile digits serrate, indentations attenuated from basis to distal part; proximal part of movable digit with a strong basal tooth which is co-adapted with a

shaft on the fixed digit [see Bertrand (1990b) or Feider and Vasilu (1970) for descriptions in others *Sellnickiella* species]. Fixed digit provided with a strong blade. Antiaxial cheliceral appendice present.

Infracapitulum and Palp (Figure 2B)

Infracapitulum proximally wide, narrowed distally, slight lips, basal width of lips narrower than infracapitulum edge. Two pairs of ventral infracapitular setae (*ma* and *mb*); a third pair (*ge*) added behind, but absent in the ♂ lacking (*ge*).

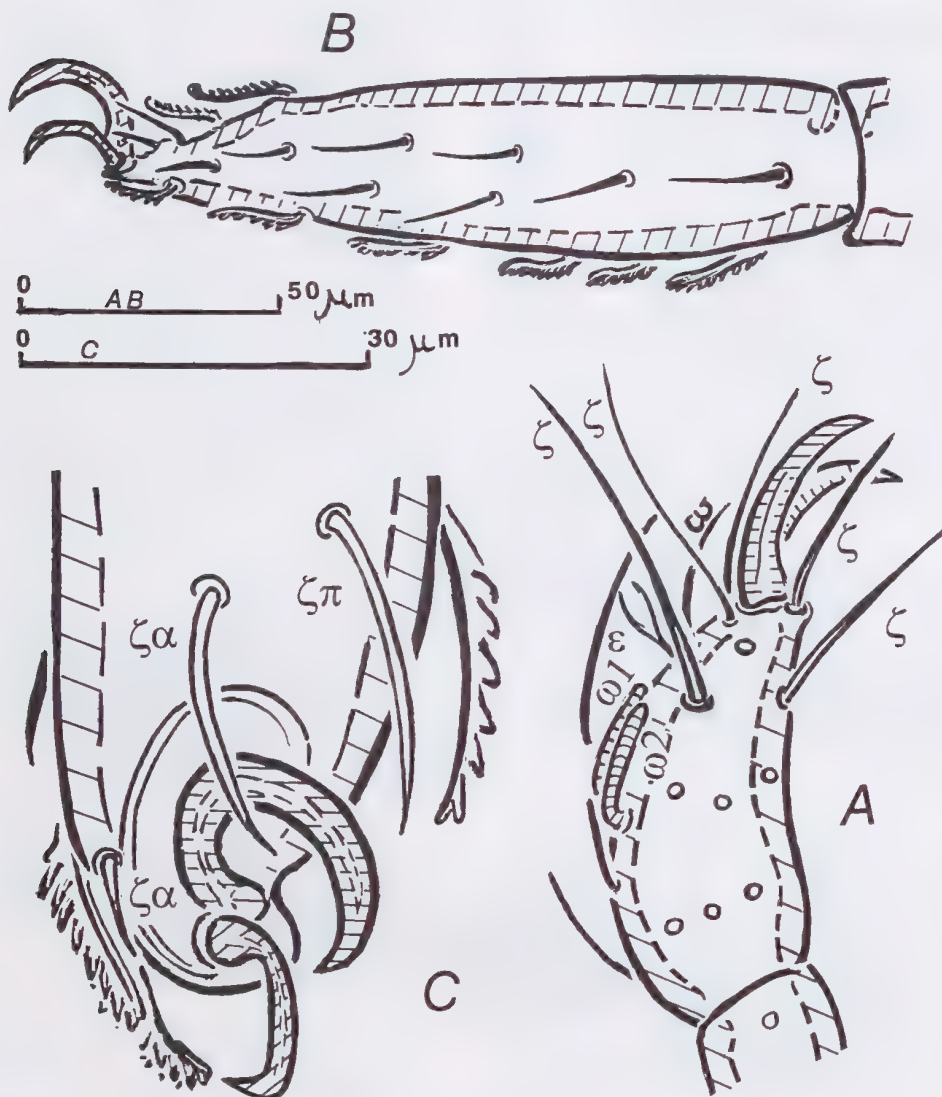


Figure 3 *Sellnickiella* (*Sellnickiella*) *biunguiculata* sp. nov.: A, tarsus I, antiaxial view; B, tarsus II, antiaxial view; C, distal part of tarsus III and claws, dorsal lateral view.

Morphology of the palp as for family, with four articles and usual chaetotaxy: 1;1;3;4+ ω ; solenidion ω tiny and dorsal.

Podosoma and Ventral Shield (Figure 1B)

Epimeral plates alveolated, except in the posterior zone where ornamentation is produced by slightly striated alveolae; strong apodemes. Epimeral plate III strongly reduced, epimera I and II developed. Epimeral plate I with the usual pore. Epimeral chaetotaxy: 15–18; 10; 6–7; 6. Ventral shield with 7–9 cuticular pores arranged in a transverse row situated behind epimera IV.

Male genital valves strongly setose, setae disposed in 4 irregular longitudinal rows. Female genital valves with only about 20 setae. When genital valves of both males and females are closed, the sagittal edges are closely appressed. Females with a narrow furrow into which anterior edge of paraprocts fit ensuring solidarity of movements of paraprocts and genital valves. Progenital chamber with two pairs of genital papillae in both sexes. Anal shields each with 3 setae. Fundamental ornamentation pattern of anal and genital valves is alveolated but pentagonal or hexagonal walls tending to disappear leaving only costules visible and giving a stellate secondary pattern.

Legs and Claws

Legs divided into trochanter, basifemur, mesofemur, telofemur, genu, tibia, tarsus and apotele. Claws of legs I–IV with only two, large unguis (10 μ m), middle unguis absent. Tarsi I–III with eupathidia. Tarsal extremities present dorsally (Figure 3C), tarsal recess visible where claws can be partially retracted (very similar to that of *Sphaerolichus barbarus* Grandjean, 1939).

Remarks

As noted above, this species is very similar to *S. (S.) womersleyi* from South Australia, but can be distinguished by features of the tarsi, dorsal shield, and fixed cheliceral digit. The principal diagnostic feature of this species is the bidactylous tarsi II–IV: it is an important character state which can be considered as autapomorphic.

Despite the unique occurrence of bidactylous legs, this species seems to form a natural group with *S. (S.) womersleyi*, *S. (S.) adalaidae* from Australia and *S. (S.) circinus* from New Zealand. This suggests that they might share a common ancestor, and that apomorphic character states of *S. (S.) biunguiculata* can be only interpreted as elements of species-level differentiation.

The claws of labidostomids, as in the Sphaerolichidae, show distinct heteronychy on legs II, III and IV, with the median unguis being the weakest and lost from leg I (Grandjean 1941).

Sellnickiella biunguiculata is unique amongst known labidostomids and shows only two claws on all legs. Of particular interest would be the nature of the tarsal claws in the immature instars: protonymphs of labidostomids present a symmetrical, tridactylous claw on leg IV. It is on this argument that Grandjean proposed that the tridactylous condition represented the primitive state, with bidactylous and monodactylous claws representing advanced states.

Also of interest is the presence of tarsal eupathidia on legs I–III: it is an usual character amongst Labidostomidae and is rare among Actinedida which usually have the eupathidia restricted to tarsi I–II. This character is also shared with Sphaerolichidae. Grandjean (1941) underlined the possible relationships between Labidostomidae and Sphaerolichidae on the basis of common primitive morphological characters. Unfortunately, the genus *Sphaerolichus* is only known from a few rare northern hemisphere species. Since Grandjean's publications (1941, 1942), new data on the lack of gland-like organs in labidostomids (notably *Sellnickiella*) clearly demonstrate that affinities between these families are strong enough to consider those Endeostigmata which lack rutella (Sphaerolichidae and Lordalycidae) are closer to the primitive Actinedida (Eupodina, Labidostomina) than to other families of this heterogeneous group.

ACKNOWLEDGEMENT

I wish to warmly thank Mark Harvey (Western Australian Museum) for providing the specimens listed above and for assistance with the preparation of the manuscript.

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Manuscript received 11 March 1997; accepted 23 July 1997.

Ticks (Acari: Ixodidae) from varanid lizards in eastern Indonesia

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During a faunal survey in eastern Indonesia conducted by staff of the Western Australian Museum and the Museum Zoologicum Bogorensis, a collection of 47 specimens of the lizard *Varanus timorensis* Gray 1831 was obtained on the islands of Timor (10°11'S, 123°43'E), Roti (10°51'S, 123°06'E), Semau (10°10'S, 123°28'E) and Savu (10°29'S, 121°55'E) during May 1989 and September–October 1990. This species weighs up to 300 grams and has a total length of up to 0.6 m. It occupies open savanna woodland at low altitudes (Schmutz and Horn 1986) and feeds on invertebrates (orthopterans and spiders) and small vertebrates (King 1993).

A smaller sample of 20 specimens of *Varanus indicus* (Daudin, 1802) was collected on the islands of Wokam (05°48'S, 134°15'E), Kai Besar (05°39'S, 132°59'E), Banda Neira (04°33'S, 129°55'E) and Yamadana (07°45'S, 131°27'E) during April 1993 and September–October 1992. This species weighs up to 2 kg and has a total length of up to 1.5 m. It inhabits areas near water and feeds on a variety of prey including crabs, other invertebrates, mammals, birds and fish (Dryden 1965; Losos and Greene 1988; King unpublished).

Ticks were collected from 17 specimens (36%) of *V. timorensis* and were mostly found attached to the neck or tail. Ticks were found on most parts of the bodies of 12 (60%) of the *V. indicus* which were examined. Ticks were found on individuals collected on all the islands listed above except Roti. All those from *Varanus timorensis* were *Aponomma soembawensis* Anastos 1956 while all those from *Varanus indicus* were *Aponomma trimaculatum* (Lucas 1878).

Aponomma soembawensis has previously been recorded only from free-living *Varanus salvator* (Laurenti 1788) from the islands of Sumba (09°37'S, 119°07'E) and Sumbawa (08°52'S, 116°50'E) and from a captive *Python reticulatus* in a zoological garden on Java (Kaufman 1972). The discovery of this species on *V. timorensis* from eastern Nusa Tenggara means that it has now been collected from a new host species and from three new localities. It only occurs in a very small area of eastern Indonesia, being distributed on natural populations of varanids on the islands of the Lesser Sundas.

Aponomma trimaculatum has been collected from a number of host species including *Varanus indicus*, several other *Varanus* species and some species of snakes (Roberts 1970). It occurs over a wide distribution ranging from Sulawesi to the Philippines, New Britain and north-eastern Australia (Kaufman 1972; Santos Dias 1993). The record of *Varanus timorensis* (Kaufman 1972) as a host for this species is incorrect as the taxonomic status of the host has recently changed and it has been recognized as a separate species, *Varanus similis* Mertens 1958, which is restricted to northeastern Australia. All new localities reported for *A. trimaculatum* here are within the known distribution of the species.

Other species of ticks collected from reptiles in eastern Indonesia also have either very restricted distributions and strong host specificity or widespread distributions and weak host specificity. The species *Aponomma komodoense* Oudemans is only found on *Varanus komodoensis* Ouwens, 1912 on Komodo Island and Western Flores, and *A. robinsoni* Warburton is only found on *Varanus komodoensis* on Komodo Island. *A. helvolum* Koch is widespread in southeast Asia and infests a number of reptilian host species including several other species of *Varanus* (Auffenberg 1981, 1988). The known host specificity of *Aponomma soembawensis* is relatively strong and its distribution is limited while the host specificity of *Aponomma trimaculatum* is weak and it has a widespread distribution.

The region in which these specimens were collected contains a high number of endemic species of mammals (Kitchener and Suyanto 1996), snakes (How and Kitchener in press) and frogs (Smith and Boeadi 1996), and is regarded as a centre of vertebrate speciation (Watts and Baverstock 1996).

ACKNOWLEDGEMENTS

We are grateful to Ken Aplin and Laurie Smith for allowing us access to specimens currently held in the reptile collection of the Western Australian Museum and to Ric How for helpful comments on an early draft of the manuscript.

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Manuscript received 17 February 1997; accepted 24 March 1997.

Liocheles extensa, a replacement name for *Liocheles longimanus* Locket, 1995 (Scorpiones: Ischnuridae)

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Since describing *Liocheles longimanus* Locket, 1995, I have become aware that the name *longimanus* was given to a subspecies of *L. australasiae* (Fabricius) by Werner (1939), thus causing a nomenclatural problem.

Werner (1939) named his new subspecies *Hormurus australasiae longimanus*, which has not been subsequently mentioned in the taxonomic literature, nor formally transferred to the genus *Liocheles* (Dr V. Fet, personal communication), of which *Hormurus* is now accepted as a junior synonym (e.g., Koch 1977). Therefore, I here transfer Werner's subspecies to the genus *Liocheles*: *Liocheles australasiae longimanus* (Werner, 1939), **comb. nov.**

Liocheles longimanus Locket, 1995, is therefore a junior secondary homonym of *Liocheles australasiae longimanus* (Werner, 1939) and thus requires a replacement name, for which I propose *Liocheles extensa* **nom. nov.**

To establish the identity of *Liocheles australasiae longimanus* (Werner), I have now examined Werner's types, which came from Montes Battak, Sumatra and are now in the collection of the Zoologisches Forschungsinstitut und Museum Koenig, Bonn.

Specimen 110 from that museum is female and 111, male; the latter has been compared with the two specimens, both male, of *L. extensa* from the Northern Territory. It is plain on inspection that the N.T. specimens have much more elongate pedipalps than Werner's specimen, and measurements of proportions confirm this. In Werner's No. 111 L/W of patella and hand are 2.14 and 3.63 respectively, compared with 2.73, 2.77 and

4.85, 5.0 for the two N.T. specimens. Though Werner's No. 111 is male, examination of the hemispermatophore was not possible, the specimen having been pinned dry originally.

The two forms are clearly distinct and it is not necessary to synonymise them. Werner's *L. australasiae longimanus* may be a valid subspecies of *L. australasiae*, but the present material is not sufficient to determine this for certain.

ACKNOWLEDGEMENTS

I wish to thank Dr Victor Fet for drawing my attention to this problem of nomenclature, he and Dr Mark Harvey for their helpful discussion, and Dr Franz Krapp of the Alexander Koenig Museum for access to the type material in his care.

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Manuscript received 13 February 1997; accepted 27 February 1997.

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Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Spelling should follow the *Concise Oxford Dictionary*.

Systematic papers must conform with the International Codes of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper. All citations, including those associated with scientific names, must be included in the references.

Manuscripts:

The original and two copies of manuscripts and figures should be submitted to the Editors, c/- Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance an IBM compatible disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. WordPerfect, Wordstar, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

Processing:

Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by the editors.

The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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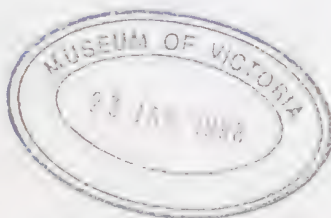
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Records of the Western Australian Museum



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Records of the Western Australian Museum

The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

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Printed and published by the Western Australian Museum

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ISSN 0312 3162

Cover: The azooxanthellate coral *Trematotrochus verconis*.
Illustration by Jill Ruse.

On the species of *Tuoba* (Chilopoda: Geophilomorpha) in Australia, New Zealand, New Caledonia, Solomon Islands and New Britain

R. E. Jones

14 Post Office Road, Dersingham, King's Lynn, Norfolk PE31 6HP, England

Abstract – The centipede genus *Tuoba* is reexamined in the Australasian region and four species are found to occur: *Tuoba sydneyensis*, *T. laticeps* *T. xylophaga* and a new species *T. pallida* from Western Australia.

INTRODUCTION

The taxonomy of the geophilomorph centipedes found in the littoral zone in Australia has a long and sometimes confusing history. Pocock (1891) described *Geophilus sydneyensis* from Port Jackson and *G. (?) laticeps* from King Island, (the (?) presumably noting that he had strong doubts about the genus) and then he transferred both species to *Necrophloeophagus* only ten years later (Pocock 1901). Specimens from Western Australia referable to both *Necrophloeophagus sydneyensis* and *N. laticeps* were then described by Attems (1911) as *G. hartmeyeri*. The latter was placed in *Nesogeophilus* Verhoeff 1924 by Attems (1929), who applied the genus name to a group of coastal centipedes with a virtually world-wide distribution. Often all the species were listed in a work with no attempt to work out the proper synonyms. Crabill (1962) synonymised *Nesogeophilus hartmeyeri* and *Necrophloeophagus laticeps* as *Nesogeophilus laticeps*, but said nothing about *Necrophloeophagus sydneyensis*.

Geophilus xylophagus, described from New Zealand by Attems (1903), was redescribed by Archey (1936), who unfortunately based his concept of the species on a mixture of *G. xylophagus* and two species now placed in *Tasmanophilus* Chamberlin 1920. Crabill (1968) showed that *Nesogeophilus* Verhoeff is a junior subjective synonym of *Tuoba* Chamberlin, a genus erected for *Tuoba curticeps* from the Solomon Islands, originally referred to the Gonibregmatidae (Chamberlin 1920). Crabill (1968) also synonymised *G. xylophagus* incorrectly with *Tuoba laticeps*. In letters written to the Tasmanian Museum and R. Mesibov in the 1970's, the late Dr Crabill showed an interest in Tasmanian specimens of *Tuoba* but was unwilling to name the local forms.

In his work on the myriapods of New Caledonia, Brölemann (1931) described a species found there

as *Algerophilus leptochilus*. He also suggested that *Geophilus xylophagus* and *G. hartmeyeri* should be included in the same group. A further species mentioned by Brölemann (1931) is *G. duponti* (Silvestri, 1897). I have seen this species and it is a completely different genus and not a *Tuoba*. Demange (1963) showed that *A. leptochilus* should really be called *Nesogeophilus leptochilus* and later (1981) stated that it also occurred around the Seychelles.

In searching through the literature in the quest for *Tuoba* and in 'disentangling' *Tuoba* from *Tasmanophilus* for a revision of the latter genus, I have examined types and unidentified material from Australia, Tasmania, New Zealand, New Caledonia, New Britain and the Solomon Islands. Here I redescribe *Tuoba sydneyensis*, *T. laticeps* and *T. xylophaga*, describe *T. pallida* sp. nov. from Western Australia and establish new synonymies for *Nesogeophilus leptochilus* and *Tuoba curticeps*. The morphological terms used are mainly those adopted by Eason (1964) and by Crabill (1968).

The following abbreviations are used:

- | | |
|------|---|
| AMNZ | Auckland Institute and Museum,
Auckland, New Zealand |
| BMNH | British Museum Natural History,
London, Great Britain |
| MCZ | Museum of Comparative Zoology,
Harvard, U.S.A. |
| NMW | Naturhistorisches Museum, Wien,
Austria |
| QVM | Queen Victoria Museum and Art Gallery,
Tasmania, Australia |
| TM | Tasmanian Museum, Hobart, Tasmania,
Australia |
| WAM | Western Australian Museum, Perth,
Western Australia, Australia |
| ZIMH | Zoologisches Institut und Museum,
Hamburg, Germany |

SYSTEMATICS

Family Geophilidae

Genus *Tuoba* Chamberlin

Tuoba Chamberlin, 1920: 35.

Nesogeophilus Verhoeff, 1924: 413. Synonymised by Attems, 1929: 184.

Algerophilus Brölemann, 1925: 250. Synonymised by Brölemann, 1925: 250.

Type species

Tuoba: *Tuoba curticeps* Chamberlin, 1920 (from Solomon Islands).

Geophilus (*Nesogeophilus*): *Geophilus* (*Nesogeophilus*) *bäckströmi* Verhoeff, 1924 (from Juan Fernandez).

Algerophilus: *Geophilus hispanica* Meinert, 1870 (from Spain, Seville, Granada).

Diagnosis

Clypeus bounded by broad paraclypeal sutures, labrum tripartite. Prosternum with chitin lines. Carpopagus structures occupy the segments to the transition (Eason, 1964). Coxopleural glands are complex, with each coxopleuron having a single large, concealed glandular crypt that is multiglandular and multicanaliculate. The pretarsal anterior parunguis is spiniform, greatly elongate and much longer than the minute posterior parunguis (Figures 3, 15, 29, 40). Anal claw present. Littoral.

Tuoba sydneyensis (Pocock)

Figures 1–11

Geophilus sydneyensis Pocock, 1891: 219; Attems 1914: 133; Attems, 1929: 326.

Necrophloeophagus sydneyensis (Pocock): Pocock, 1901: 461.

Geophilus (*Aporophilus*) *sydneyensis* (Pocock): Attems, 1903: 262.

Geophilus hartmeyeri Attems, 1911: 158. figs 11, 12 (in part); Attems, 1914: 127 (in part) Attems 1914: 133; Chamberlin, 1920: 53 (in part) (synonymised by Crabill, 1968: 345).

Tuoba curticeps Chamberlin, 1920: 35; Attems, 1929: 338. **New synonymy.**

Geophilus (?) *sydneyensis* Pocock: Chamberlin, 1920: 54.

Nesogeophilus hartmeyeri (Attems): Attems, 1929: 186 (in part); Attems, 1947: 118 (in part).

Algerophilus leptochilus Brölemann, 1931: 311. **New synonymy.**

Algerophilus hartmeyeri Brölemann, 1931: 314, by implication.

Nesogeophilus leptochilus (Brölemann): Attems, 1947: 118; Demange 1963: 87.

Material Examined

Syntype of *Geophilus sydneyensis* Pocock

1 ♂, Inner Double Bay, Port Jackson, New South Wales, Australia (BMNH, accession no. BM 1879.5.20.13).

Types of *Geophilus hartmeyeri* Attems

Lectotype, Denham, Shark Bay, Western Australia, Australia (designated by R. Crabill, 12 May 1960) (ZIMH).

1 paratype (A), same data (designated by R. Crabill, 12 May 1960) (ZIMH).

1 syntype, Denham, Shark Bay, Western Australia, Australia (NMW, 2006).

Paratype of *Tuoba curticeps* Chamberlin

1 ♀ Wainoni Bay, Solomon Islands, W.M. Mann (MCZ TC-138(2167) and slide 2167a). The holotype of *Tuoba curticeps* has been lost.

Types of *Algerophilus leptochilus* (Brölemann)

The types of this species could not be found in the Muséum National d'Histoire Naturelle, Paris. However I was able to examine samples of *Nesogeophilus leptochilus* which Demange used for his 1963 paper.

Other Material

Australia: Western Australia: 13 ♂, 8 ♀, Eagle Bluff, 26°06'S, 113°35'E, 25–29 November 1991, seagrass litter from littoral zone, M.S. Harvey and M.E. Blosfelds (WAM 92/1050–71); 3 ♂, 2 ♀, Eagle Bluff, 26°06'S, 113°35'E, 25–29 November 1991, under rocks, littoral zone, M.S. Harvey and M.E. Blosfelds (WAM 92/1072–6); 2 ♀, Mandu Mandu Beach, Cape Range National Park, 29 February 1986, on beach, under crab exuviae, J.M. Waldock (WAM 92/1112–3); 2 ♂, 1 ♀, Rosemary Island, 6 August 1985, R.P. McMillan (WAM 92/1386–8).

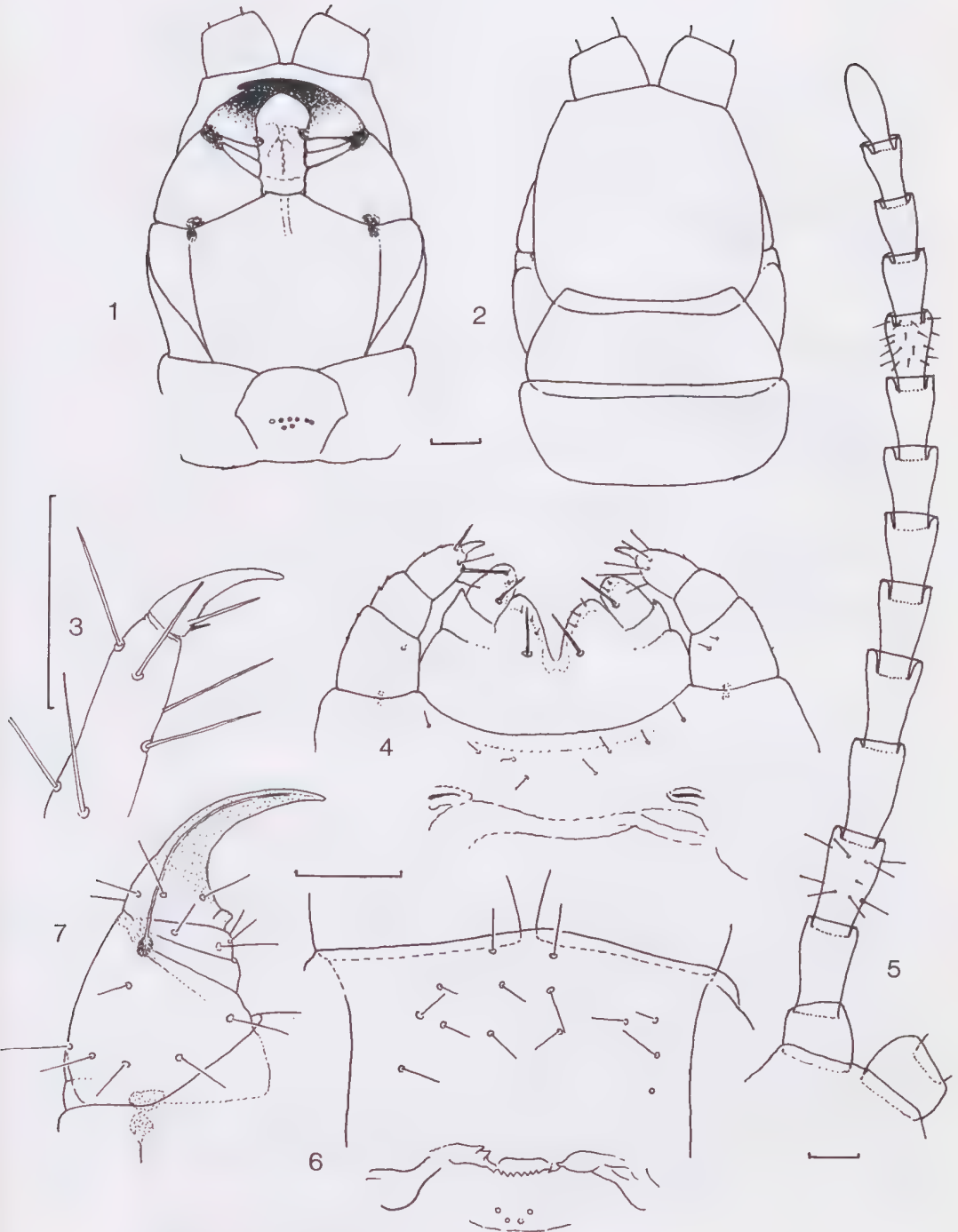
Papua New Guinea: New Britain: 5 ♂, 2 ♀, Hoskins, 23 May 1997, on sandy beach under small logs, R.E. Jones (R.E. Jones collection).

Description

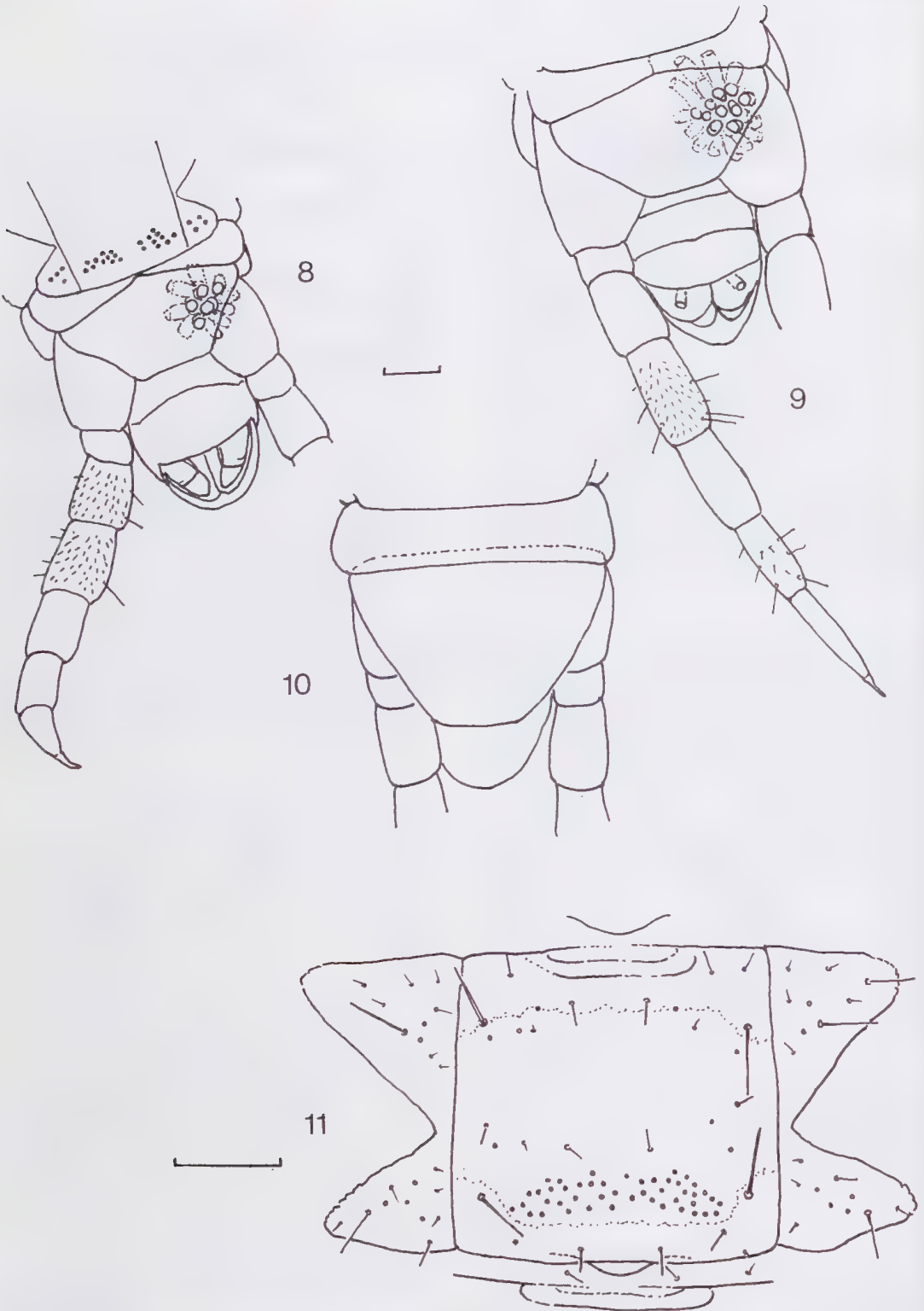
Maximum length 32 mm.

Number of leg-bearing segments 39–55 (43–49 ♂, 43–55 ♀ in Australia, 39–41 ♂, 41–43 ♀ in New Caledonia, 45 ♂, 45–47 ♀ in New Britain and 47 ♂, 49 ♀ in the Solomon Islands). The numbers of legs for males and females in this and the following species will no doubt be extended as more are collected.

Colour orange yellow throughout. Antennae: about 5 times the length of the head capsule, first segment as broad as long then from the second to the penultimate about twice as long as broad, last segment greatly exceeded by the previous two (Figure 5). Setae moderate throughout. Head



Figures 1-7 *Tuoba sydneyensis* (Pocock): 1, head from below; 2, head from above; 3, claw of left walking leg; 4, first and second maxilla from below; 5, antenna from below; 6, clypeus; 7, forcipule from below. Scale lines = 0.1 mm.



Figures 8–11 *Tuoba sydneyensis* (Pocock): 8, last segment from below, ♂; 9, last segment from below, ♀; 10, last segment from above; 11, sternite of segment 8. Scale lines = 0.1 mm.

capsule as long as broad, the sides being convex (Figure 2). Clypeus 1+1 postantennary setae and 6+6 midlabral setae, there is a slight area of reduced areolation on either side in front of the labrum. Labrum tripartite, 7–9 teeth on the midpiece and 2+2 on the sidepieces (Figure 6). First maxilla 3+3 setae on the teleopodites and 4+4 setae on the coxal projections, (in both cases there is 1 large seta and the rest are very small), there is a small lappet on the teleopodite. Second maxilla bears a simple claw surrounded by a whorl of six or seven setae (Figure 4). Forcipules (prehensors / poison claws) with concavity of claw smooth and a small basal node, reaching almost to the front of the head capsule when closed. Chitin lines complete or nearly so (Figures 1, 7). Sternites: pores throughout forming a ventral band on the sternite which becomes two separate groups by the end of the animal, also on the procoxa and metacoxa plus a few scattered across the front of the anterior segments. Areolation less than in *T. laticeps* forming a band at the dorsal and later the ventral areas of the sternite. Carpophagus structure present until the transition, the fossa being over half as wide as the sternite at its full extent (Figure 11). Metatergite trapeziform, wider than long (4:3), sides slightly convex (Figure 10), metasternite trapeziform, the sides being slightly concave. Coxopleuron contains about 20–35 glands in a rosette arranged around a pit. Last legs of female two times the length of the penultimate legs, femur 2:1 length to breadth (Figure 9), last legs of male fatter, femur about 1.5 : 1 length to breadth (Figure 8). Anal pores present. Claws present on last legs.

Remarks

Brölemann's excellent drawings and the specimens of Demange that I have seen show that it is clearly a species of *Tuoba*. *Nesogeophilus leptochilus* has a lower number of leg pairs than the *Tuoba sydneyensis* of Australia (39–43 pairs) but I can find no other differences between them and am inclined to amalgamate them as one species, *T. sydneyensis*. Likewise *T. curticeps*, of which the type is lost but a paratype remains, shows the characters associated with *T. sydneyensis* and I have also amalgamated them as *T. sydneyensis*. The specimens collected from New Britain also appear to be *T. sydneyensis* with 45–47 pairs of legs. The only difference being the pretarsal anterior parunguis which is as long as the claw in one specimen and may represent the unworn state.

Tuoba laticeps (Pocock)

Figures 12–23

Geophilus (?) *laticeps* Pocock, 1891: 220, pl. 12, fig. 6, 6a; Chamberlin, 1920: 54.

Necrophloeophagus laticeps (Pocock): Pocock, 1901: 463.

Geophilus (*Aporophilus*) *laticeps* (Pocock): Attems, 1903: 261.

Geophilus hartmeyeri Attems, 1911: 158. figs 11, 12 (in part); Attems, 1914: 127 (in part); Attems 1914: 130; Chamberlin, 1920: 53 (in part) (synonymised by Crabill, 1968: 345).

Geophilus laticeps Pocock: Attems 1914: 130; Attems, 1929: 328.

Nesogeophilus hartmeyeri (Attems): Attems, 1929: 186 (in part). (Attems): Attems, 1947: 118 (in part).

Algerophilus hartmeyeri Brölemann: 1931 by implication.

Nesogeophilus laticeps (Pocock): Crabill, 1962: 506; Mesibov, 1986: 54.

Tuoba laticeps (Pocock): Crabill 1968: 345.

[*Tuoba xylophagus*: Crabill, 1968, not (Attems) 1903 (incorrect synonymy by Crabill, 1968: 345).]

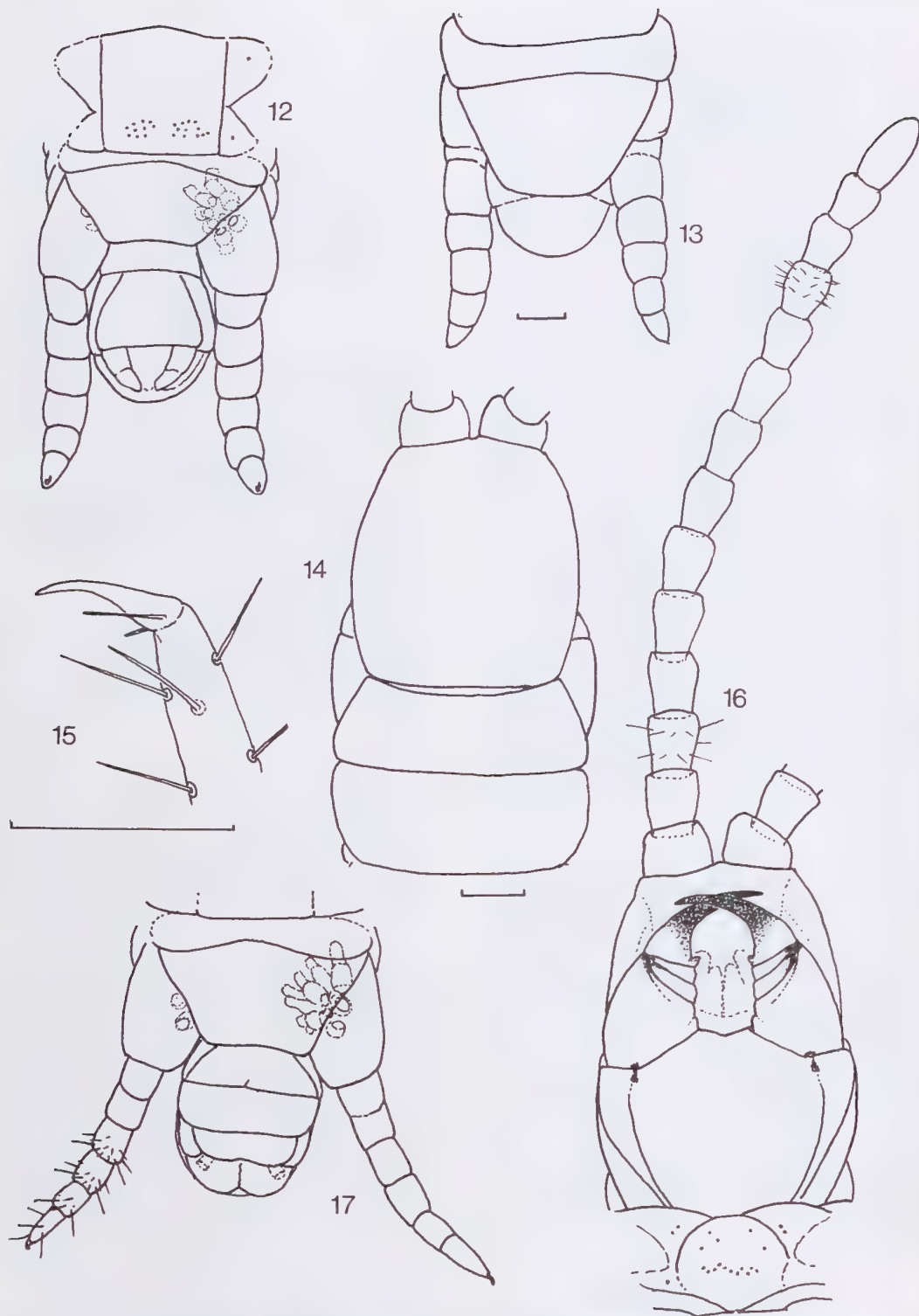
Material Examined

Holotype of *Geophilus laticeps* Pocock
♀, King Island, Bass Strait, Australia, A. Dendy (BMNH, accession no. BM 1888.144).

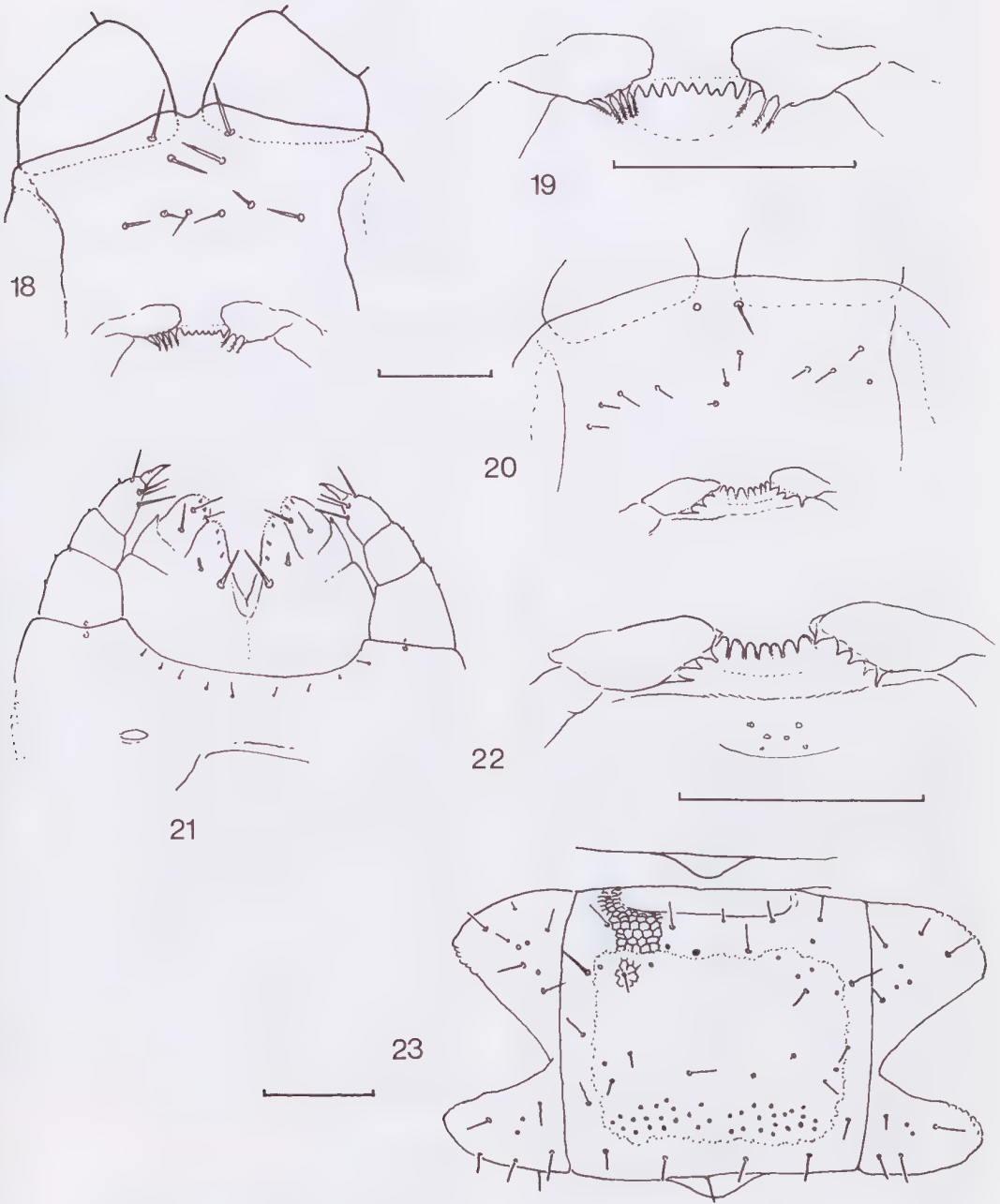
Syntype of *Geophilus hartmeyeri* Attems
1, Albany, Western Australia, Australia (NMW, 2007).

Other Material

Australia: Tasmania: 1 ♀, Midway Point, S.E. Tas., 4 April 1973, under rocks at high tide level on shore, Mr G. Prestedge [det. *Tuoba* sp. Dr R.E. Crabtree (sic), 1984] [TM J3139/2, slide prepared by R.E. Crabill (labelled 74.II.7/GC-6)]; 1 ♂, 10 ♀, Midway Point, S.E. Tas., 4 November 1973, under rocks on sand, at high water mark, under a causeway (= the second causeway), Mr G. Prestedge [det. *Tuoba* sp. Dr R.E. Crabtree (sic), 1984] (TM J3140); 2 ♂, 1 ♀, Brick Maker's Beach, Municipality of Circular Head, 21 January 1995, under stones on fine shell gravel, rocky shore, upper barnacle zone and black obtuse "*Littorina*", S.J. Lewis (QVM 23:17732); 6 ♂, 5 ♀, E. end of Bay just West of Penguin, 30 January 1995, under stones, strand line by rocky outcrop S.J. Lewis (QVM 23:17730); 6 ♂, 5 ♀, N. end of Ralphs Bay, Lauderdale, Hobart, 25 January 1995, under stones, strandline, stony beach, S.J. and J.G.E. Lewis (QVM 23:17733); 1 ♂, N. corner Prosser Br. Bay, Orford, 26 January 1995, in small cave 1 x 1 ♂, under rock + woodlice, crabs, sand hoppers, J.G.E. Lewis (QVM 23:17735); 2 ♂, 2 ♀, 2 ♂, 2 ♀, Swansea, S. most part Nine Mile Beach by small rocky prom., 27 January 1995, under stones, drift zone with woodlice, sandhoppers, S.J. Lewis (QVM 23:17736).



Figures 12–17 *Tuoba laticeps* (Pocock): 12, last segment from below, ♂; 13, last segment from above, ♂; 14, head from above; 15, claw of right walking leg; 16, head and antenna from below; 17, last segment from below, ♀. Scale lines = 0.1 mm.



Figures 18–23 *Tuoba laticeps* (Pocock): 18 and 20, clypeal regions; 19 and 22, labra; 21, first and second maxilla from below; 23, sternite of segment 9. Scale lines = 0.1 mm.

Description

Maximum length 23 mm.

Number of leg-bearing segments 43–59 (43–59 ♂, 45–59 ♀).

Colour orange yellow throughout. Antennae about 3 times the length of the head capsule, the first segment broader than long, the second longer than broad (1.5 : 1) segments gradually becoming shorter until length and breadth are about equal. Last segment about as long as the two preceding. Setae moderate throughout (Figure 16). Head capsule as long as broad, the sides convex (Figure 14). Basal plate present. Clypeus with two postantennal setae and two to three intermediate setae with a row of six to eleven setae below them (Figures 18, 20). Labrum tripartite, seven or eight tubular teeth on the mid-piece and up to five long thin filaments (fimbriae) arising from broad bases and having the tips divided into smaller filaments. (This feature is not always visible and may be absent, only triangular teeth being seen in some slide preparations) (Figures 19, 22). First maxilla with membranous tips to the telopodite and coxal projections, small lappet on the telopodite, setae 3+2 on the telopodites (plus 2+2 micro-setae) and 2+2 (plus 3+3 micro-setae) on the coxal projections. Second maxillae bear a ring of 4+4 setae at the tip and 9 setae on the syncoxite. Claw of second maxilla appears to be simple with a curved tip but it may represent a fusion of elements. Syncoxite entire (Figure 21). Forcipules with concavity smooth and a small basal node, reaching just short of the head. Chitin lines complete or nearly so (Figure 16). Sternites, segments with very pronounced areolation until the transition. After segment four or five there is a central smooth rectangle which also contains a ventral band of pores until about segment 14 when it divides into two. Pores also on the procoxa and metacoxa plus a few scattered across the front of the anterior part of the segments. The carpophagus structure is present up until the transition, (about segment 11). At its maximum the carpophagus fossae are about two thirds of the breadth of the sternite (Figure 23). Last segment, metatergite practically semicircular (Figure 13), metasternite trapeziform, the sides being slightly concave. The presternite is divided. Coxopleuron contains a group of about seven to nine coxal glands opening into a pit. Last legs of the female only slightly fatter and longer than the penultimate legs (Figure 17) and the last legs of the male again slightly fatter still (Figure 12). Anal pores present. Claws present on last legs.

Tuoba xylophaga (Attems)

Figures 24–34

Geophilus xylophagus Attems, 1903: 273; Attems

1914: 127; Chamberlin, 1920: 53; Archey, 1936: 50, p 12, fig. 7.

Nesogeophilus xylophagus (Attems): Attems, 1929: 185; Attems, 1929: 118.

Algerophilus xylophagus Brölemann, 1931: 314, by implication.

Tuoba xylophagus (Attems): Crabill, 1968: 345 (as a synonym of *Tuoba laticeps*).

Material Examined

Holotype

New Zealand, 1903 (NMW, 318, 2 slides in poor condition).

Other Material

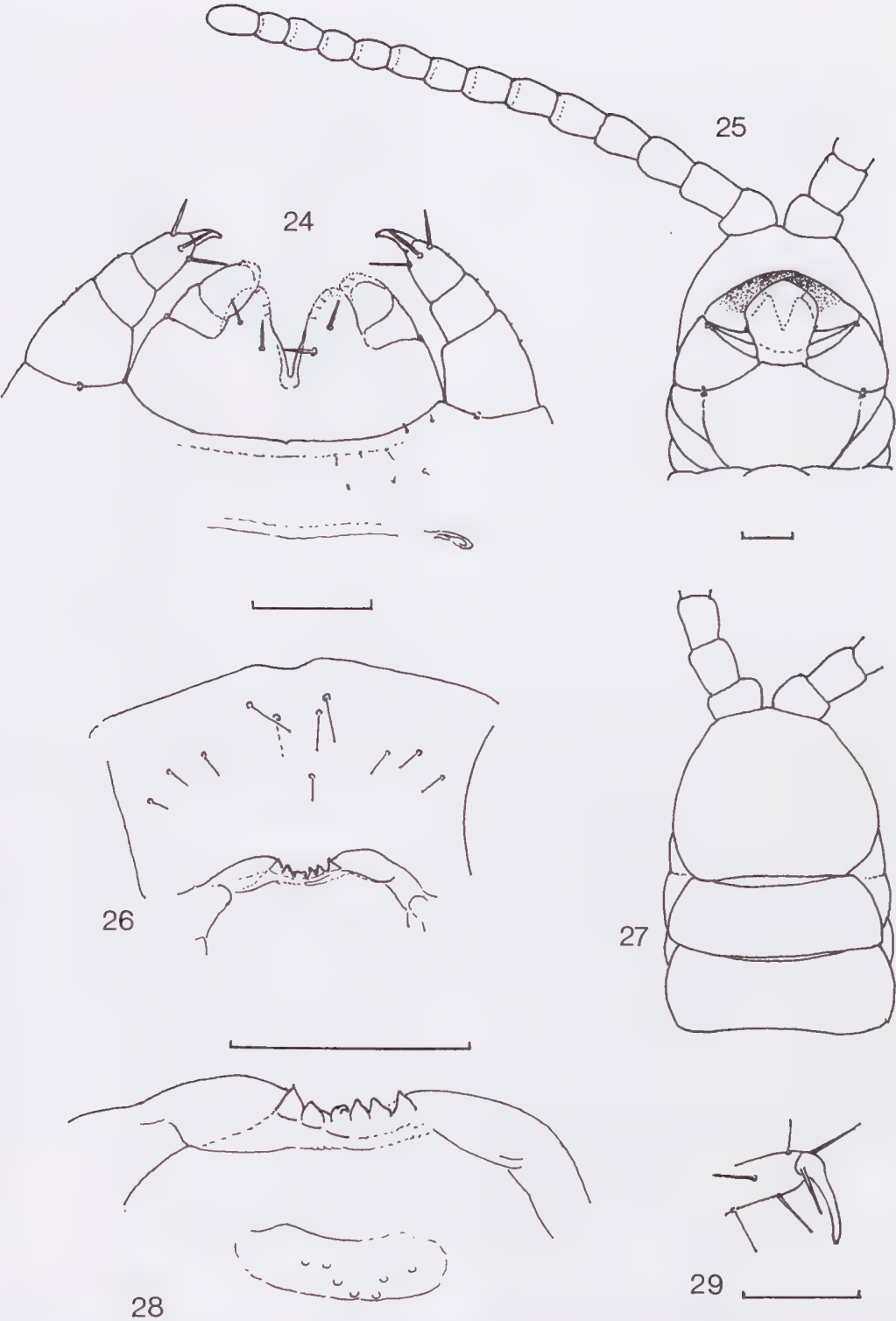
New Zealand: 1 ♂, Muriwai, Waitemata Co., North Island, 7 October 1931, G. Archey (AMNZ 812, plus slide No. 2); 1 m. Muriwai, Waitemata Co., North Island, 7 October 1931, G.A. (AMNZ 813, plus slide No. 3); 1 ♀, Whangaeri, October 1932, Chas. E. Clarke (AMNZ 846, AMNZ 811 Slide No 1); 5 ♂, 1 ♀, Muriwai, Waitemata Co., North Island, 7 October 1931 G. Archey (AMNZ 847); 1 ♂, Waikewau Beach, N. E. Coromandel, 15 November 1932 G. Archey (AMNZ 848); 1 ♂, 1 ♀, Brighton Beach, on dead bird (AMNZ 850, no. 101); 1 ♂, 1 ♀, Helena Bay, Whangarei, Whangarei Co. North Island 8 January 1935, on seaweed washed ashore, E.D. Pritchard (AMNZ 852); 1 ♂, Christchurch, South Island, 1902, Sumner (AMNZ 853); 1 ♀, Ahipara, Mangonui Co. North Island, 25 February 1925, G.A. (AMNZ 854); 1 ♀, Oakura Taranaki Co. North Island, 10 June 1931, G. Archey (AMNZ 855, det. *Otagophilus xylophagus* Attems; as far as I can find out *Otagophilus* was never used in any publication); 5 ♂, 2 ♀, Punakaiki, 21 September 1974, supralittoral sand (P.M. Johns collection, Canterbury University); 5 ♂, 3 ♀, Carters Beach, Westport, 27 February 1978, logs on sand (P.M. Johns collection, Canterbury University); 2 ♂, 1 ♀ Brue Bay, Sth Westland, 19 January 1979, supralitt. (P.M. Johns collection, Canterbury University); 6 ♂, 2 ♀, 2 km N. of Karkoura, 27 August 1984, fine stony beach, driftwood, (P.M. Johns collection, Canterbury University); 1 ♂, locality unknown (AMNZ 851).

Description

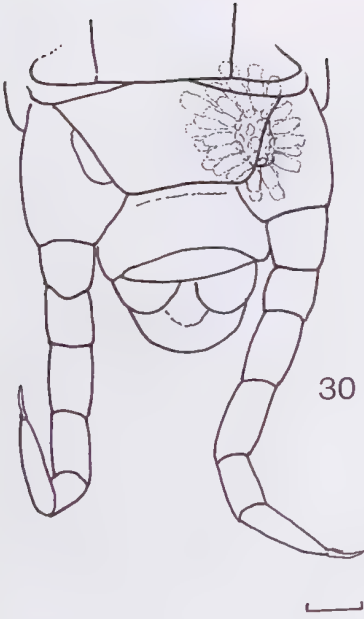
Maximum length 45 mm.

Number of leg-bearing segments 57–67 (57–65 ♀, 61–67 m).

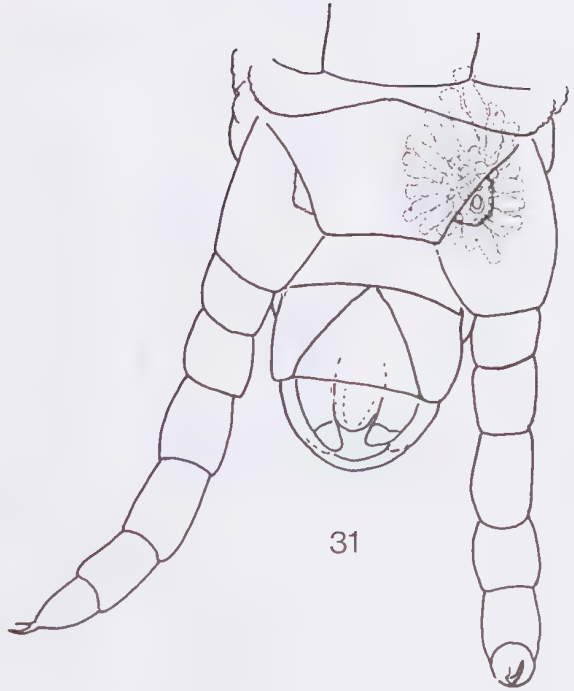
Colour orange yellow throughout. Antennae about 4 times the length of the head capsule, first segment as long as broad thereafter longer than broad decreasing until the penultimate which is barely longer than broad. Last segment slightly



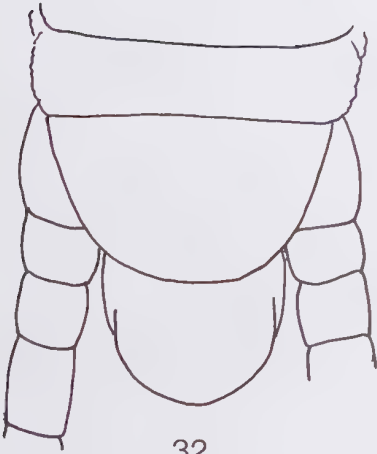
Figures 24–29 *Tuoba xylophaga* (Attems): 24, first and second maxilla from below; 25, head and antenna from below; 26, clypeus; 27, head from above; 28, labrum; 29, claw of left walking leg; Scale lines = 0.1 mm.



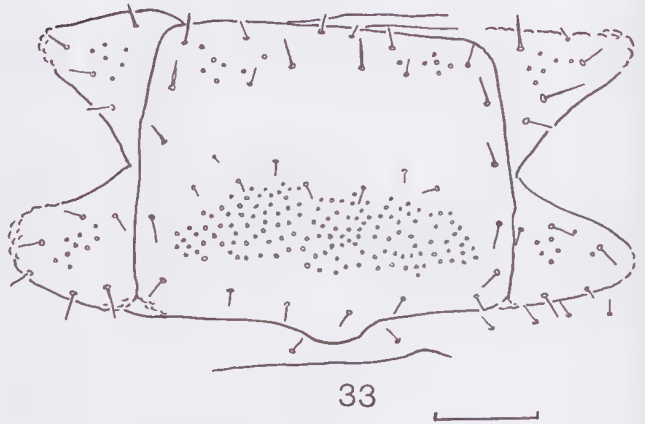
30



31



32



33



34

Figures 30–34 *Tuoba xylophaga* (Attems): 30, last segment from below, ♀; 31, last segment from below, ♂; 32, last segment from above, ♂; 33, sternite of segment 19, 34, labrum. Scale lines = 0.1 mm.

shorter than the last two. Setae moderate throughout (Figure 25). Head capsule as long as broad the sides being convex (Figure 27). Basal plate present. Clypeus with 2+2 postantennary setae, 3+3–4 medial setae and 1–2 prelabral seta (Figure 26). Labrum with 4–6 pointed teeth on the midpiece and 1–3 on the side pieces (Figures 28, 34). First maxilla with tips membranous and ciliate and 2–5+2–4 setae (plus micro-setae) on the central lobes and 0–2+0–3 setae (plus micro-setae) on the telopodites. Very rudimentary lappets on the telopodites. Secondary maxilla with a simple claw half the length of the last telomere which also bears 3 setae (Figure 24). Forcipules rounded with the concavity smooth and no basal node, reaching to just short of the head capsule when closed. Chitin lines complete or nearly so (Figure 25). Sternites with pores on all segments in a spindle shaped group in the hind part of each segment also on the procoxa and metacoxa plus a few scattered across the front of the anterior segments. Carphophagus structure from the second to about segment twenty, the fossae occupying just under half the width of a sternite at their largest (Figure 33). Metatergite D-shaped, wider than long, the convex sides converging posteriorly and the posterior edge being straight or nearly so (Figure 32). Metasternite is rhomboidal, wider than long, all edges being slightly concave. Coxal glands opening into a pit partially covered by the metasternite, there being about 30 per side. The last legs of the female not much longer than the walking legs (Figure 30), the last legs of the male slightly fatter than those of the female, but not much (Figure 31). Anal pores present. Claws present on last legs.

Remarks

Archey retained *xylophagus* in *Geophilus* (1936), in which he also described two species which are now regarded as *Tasmanophilus* (Jones, in preparation). He muddled specimens of this species with some *Tasmanophilus spenceri* and *Tasmanophilus* sp. which gave rise to the error that there were "oval median depressions present, deep on anterior segments, shallower on middle ones" in this genus. His paper also gave a diagrammatic representation of the last segment but the coxal pores were interpreted incorrectly.

The name *xylophagus* changes to *xylophaga* to conform to the gender of the genus.

Tuoba pallida sp. nov.

Figures 35–43

Material Examined

Holotype

♀, Rockingham, Penguin Island, Western Australia, Australia, 2 July 1980, Silver Gull nest

litter *Larus novaehollandiae*, S. and J. Peck, SBP WA 80 (WAM 92/1358).

Paratypes

Australia: Western Australia: 1 ♂ 3 ♀, same data as holotype (WAM 92/1359–61); 1 ♂, 1 ♀, Windy Harbour, 27 km S. of Northcliffe, 8 July 1980, coast shrub litter, S. and J. Peck, SBP WA 101 (WAM 92/1648–9).

Description

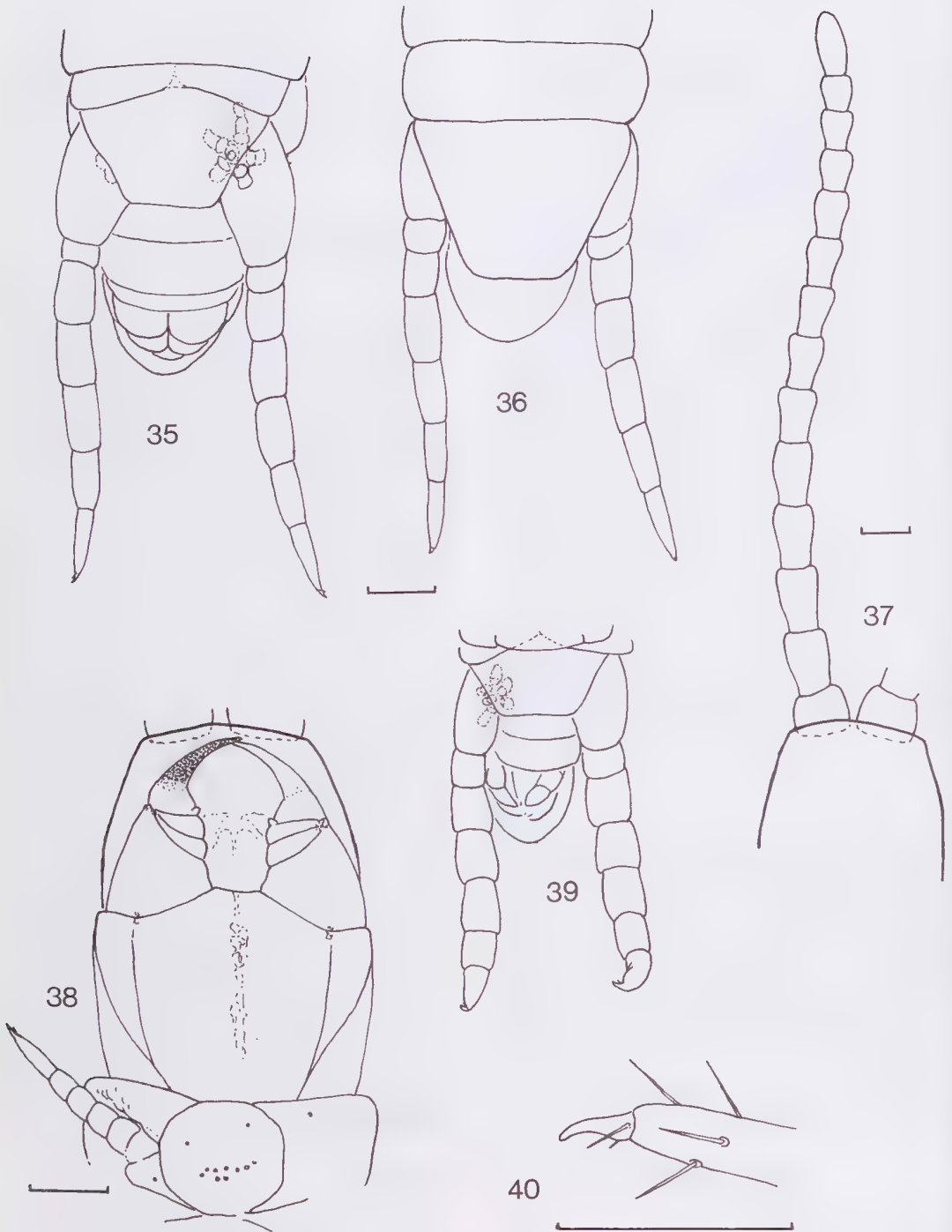
Maximum length 25 mm.

Number of leg-bearing segments 55–59 (55 ♂, 57–59 ♀).

Colour white throughout. Head capsule slightly longer than wide, anteriorly narrowed, the sides convex. Antennae about 4 times the length of the head capsule. The first segment broader than long, the second longer than broad (1.5:1) decreasing slightly until the penultimate segment, the last segment being just shorter than the preceding two. Sparsely covered with setae throughout (Figure 37). Clypeus consists of 2+2 anterolateral setae and a band of 3+4 intermediate setae. There are two areas of reduced areolation just distal of the labrum. Labrum not very clear but it is tripartite, with at least four teeth on the centre piece (Figure 43). First maxillae with ciliate tips to the telopodites and coxal processes and a small lappet on each side, setae are 3+3 on the telopodites and 4+4 on the processes. Second maxillae with claws that appear to end in a bristle and surrounded by 4 or 5 setae (Figure 41). Forcipules reach to just short of the head capsule when closed, small basal nodes present. Chitin lines complete or nearly so (Figure 38). Carphophagus structure reduced and almost absent, very hard to see. Pores on every segment as a posterior band except for the first where they form a circular group. Also pores on the procoxa and metacoxa and a few scattered across the front of the segment (Figure 42). Metatergite rhomboidal, the sides and posterior edge nearly straight (Figure 36), metasternite trapeziform, the sides being slightly concave. Coxal glands opening into a pit partially covered by the metasternite, there being about 6–8 per side. Last legs of male slightly swollen, about as long as the walking legs (Figure 39), less swollen in the female (Figure 35, 36). Anal pores are apparently not present. Claws present on last legs.

Remarks

The four species of littoral centipedes which are known to occur in the region can easily be separated by leg numbers and the size of the last pair of legs. *Tuoba sydneyensis* has 39–55 pairs of legs and the last legs are comparatively long. *T. laticeps* has 43–59 pairs of legs but the last legs are



Figures 35–40 *Tuoba pallida* sp. nov.: 35, last segment from below, ♀; 36, last segment from above, ♀; 37, antenna; 38, head from below; 39, last segment from below, ♂; 40, claw of right walking leg; Scale lines = 0.1 mm.



Figures 41-43 *Tuoba pallida* sp. nov.: 41, first and second maxilla from below; 42, sternite of segment 9; 43, clypeus. Scale lines = 0.1 mm.

comparatively short and not much longer than the walking legs. The antennae differ in length being much longer in the former but in preserved specimens the antennae often shrink in length, the antennomeres being telescoped inside one another.

T. xylophaga, with 57-67 pairs of legs, is found only in New Zealand where it should not cause any problems. *T. pallida* has been found in Western Australia so far. It has 55-59 pairs of legs, comparatively long thin last legs coupled with its very pale, almost white, colouring make it easy to identify. However, at the present state of knowledge of Australian centipedes, it should be borne in mind that there may be similar species which have not yet been recorded.

REMARKS

About 20 species of the genus have now been described but it is still in a taxonomic muddle, there are probable synonyms amongst them and some have been wrongly attributed to *Tuoba*. In *Tuoba* a number of coxalpleural glands should open into a pit or crypt. There are several other species recorded from the Pacific basin all of which may or may not be valid. *Nesogeophilus annamiticus* from Indochina seems to be very similar to *T. sydneyensis* from the literature description and would repay a look.

ACKNOWLEDGEMENTS

In preparing this paper I received a lot of help from museums and other taxonomists. I should

like to thank Dr H. Levi and his staff of the Museum of Comparative Zoology, Harvard, J.W. Early of the Auckland Museum, Dr J.-P. Mauries of the Museum National d'Histoire, Paris, Dr J. Gruber of the Naturhistorisches Museum Wien, Dr H. Dastych of the Zoologisches Museum, Hamburg, Dr T. Kingston and staff of Queen Victoria Museum and Art Gallery, Launceston, Tasmania and P.D. Hillyard of the British Museum. I should also like to thank Dr J.G.E. Lewis, Dr R. Mesibov, Prof. A. Minelli, Dr E.H. Eason and Dr A.G. Irwin for help and encouragement and Dr M.S. Harvey of Western Australian Museum for the loan that started the whole thing. Finally I should like to thank Norfolk Museum Service for research facilities.

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The water mite family Limnesiidae from northern and Western Australia (Acari: Actinedida), with a description of two new species

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Abstract – Two new species, *Limnesia rubra* and *Physolimnesia katherine*, are described from the Northern Territory, Australia. *Timmsilimnesia prendens* is synonymized with *Limnesia inga*. Additional taxonomic characteristics are given for *L. parasolida* and *L. solida*. Furthermore, new records are presented from the Northern Territory and Western Australia for a number of *Limnesia* species known from other regions of Australia.

INTRODUCTION

The family Limnesiidae is represented in Australia by five genera: *Heterolimnesia*, *Limnesia*, *Physolimnesia*, *Timmsilimnesia* and *Tubophorella* (Cook, 1986). The most species-rich genus is *Limnesia*, with 25 species known from Australia so far.

Limnesiid water mites occur in nearly every lentic water of Northern Territory and Western Australia. Together with members of the genus *Arrenurus* (Smit, 1997), they belong to the most abundant water mites of these type of waters (personal observation).

In this study, two new species are described, *Limnesia rubra* and *Physolimnesia katherine*. New records are presented of *Limnesia inga* K.O. Viets, *L. lebangensis* Piersig, *L. longigenitalis* Lundblad, *L. maceripalpis* K.O. Viets, *L. parasolida* K.O. Viets, *L. solida* Lundblad and *Timmsilimnesia prendens* K.O. Viets. *Timmsilimnesia prendens* proved to be the male of *Limnesia inga*, a species previously known only from the female; the new name is *Timmsilimnesia inga* (K.O. Viets). Additional taxonomic characteristics are given for two previously inadequately described species, *L. parasolida* and *L. solida*.

MATERIAL AND METHODS

All material has been collected by the author. Holotypes and paratypes from the Northern Territory have been deposited in the Northern Territory Museum (Darwin) (NTM). Additional paratypes have been deposited in the Western Australian Museum (Perth) (WAM) and the Zoological Museum of the University of Amsterdam (ZMA). All non-type material has been placed in the ZMA.

Measurements of palp and leg segments are dorsal lengths. The body length is measured dorsally from unmounted specimens. Measure-

ments of paratypes are given in brackets. The following abbreviations have been used: PI-PV palp segments 1–5; I-leg-5 fifth segment of first leg.

SYSTEMATICS

Genus *Limnesia* Koch

Limnesia Koch, 1836: 19.

Limnesia (Limnesia) lebangensis Piersig

Limnesia lebangensis Piersig, 1906: 348; Walter, 1928: 73; Walter, 1929: 228; K. Viets, 1935: 607; Uchida, 1935: 121; Halik, 1941: 109; K.O. Viets, 1959: 422; Imamura, 1964: 70; Cook, 1967: 87; Lundblad, 1969: 334; Prasad, 1974: 62; K.O. Viets, 1975: 93; Bisht, 1979: 89; Khatoon and Ali, 1989: 613; Smit, 1992: 95.

Limnesia gentilis Koenike, 1906: 124.

Limnesia gentilis indica K. Viets, 1926: 378.

Material Examined

Australia: Northern Territory: 1 ♀, Lake Jabiru, Jabiru, 20 July 1994; 6 ♂, 5 ♀, 1 nymph, billabong Yellow Waters, Kakadu National Park, 21 July 1994.

Remarks

Unlike specimens from eastern Australia, which have red chitinated parts (Halik, 1941; personal observation), those of Northern Territory have brown chitinated parts.

Distribution

Previously reported from New South Wales (Halik, 1941) and Queensland (Smit, 1992). *L. lebangensis* has a very wide distribution, and is known from Taiwan, Singapore, Thailand, India, Pakistan, Sri Lanka and Indonesia.

Limnesia (Limnesia) longigenitalis Lundblad

Limnesia longigenitalis Lundblad, 1941a: 114; Lundblad, 1947: 42; Smit, 1992: 95.

Material Examined

Australia: Western Australia: 4 ♂, 12 ♀, 2 nymphs, ditch pastoral land, Peaceful Bay, southwest of Denmark, 30 August 1994; 1 ♀, Lake Seppings, Albany, 31 August 1994.

Remarks

The females of this study measure 1188–1296 in length, the males 698–737 in length. Lundblad (1947) mentioned the following lengths: male 690, female 1345.

Distribution

Previously reported from Victoria (Lundblad, 1947) and New South Wales (Smit, 1992). In this study, the species has been found only in the southwestern part of Western Australia.

Limnesia (Limnesia) maceripalpis K.O. Viets

Limnesia maceripalpis K.O. Viets, 1975: 93; K.O. Viets, 1984: 421; Cook, 1986: 77.

Material Examined

Australia: Northern Territory: 1 ♀, Radon Springs, Kakadu National Park, 19 July 1994; 1 ♂, Baroalba Springs (Gubarra), Kakadu National Park, 20 July 1994; 2 ♂, 2 ♀, 1 nymph, Lake Jabiru, Jabiru, 20 July 1994; 2 ♂, pool Twin Falls, Kakadu National Park, 23 July 1994; 1 ♀, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 2 ♂, 1 ♀, Southern Rockhole, Katherine Gorge National Park, 27 July 1994; 6 ♂, 3 ♀, plunge pool Edith Falls, Katherine Gorge National Park, 30 July 1994.

Western Australia: 1 ♀, Palm Pool, Millstream-Chichester National Park, 15 August 1994; 1 ♂, 3 ♀, pond Snake Creek, Millstream-Chichester National Park, 17 August 1994; 3 ♀, Ashburton River, at crossing with North West Coastal Highway, 18 August 1994; 3 ♀, 1 nymph, Fortescue River, at crossing with North West Coastal Highway, 18 August 1994.

Remarks

The largest male of this study measured 1320 in length, the largest female 1536. Cook (1986) gave the following measurements: males 760–851 and females 927–1075.

Distribution

Previously reported from Queensland (K.O. Viets, 1975; Cook, 1986) and the Northern Territory (K.O. Viets, 1984).

Limnesia (Limnesia) parasolida K.O. Viets

Figure 1

Limnesia parasolida K.O. Viets, 1984: 419; Cook, 1986: 76; Smit, 1992: 95.

Material Examined

Australia: Northern Territory: 4 ♂, 7 ♀, Radon Springs, Kakadu National Park, 19 July 1994; 8 ♂, 6 ♀, billabong Nourlangie Creek, Kakadu National Park, 20 July 1994; 3 ♂, 2 ♀, Lake Jabiru, Jabiru, 20 July 1994; 19 ♂, 24 ♀, 3 nymphs, Baroalba Springs (Gubarra), Kakadu National Park, 20 July 1994; 2 ♀, Mardugal Billabong, Kakadu National Park, 21 July 1994; 3 ♀, 5 nymphs, pond in Jim Jim Creek, at Jim Jim Crossing, Kakadu National Park, 22 July 1994; 1 ♀, Home Billabong, Kakadu National Park, 22 July 1994; 8 ♂, 15 ♀, pool near Jim Jim Falls, Kakadu National Park, 23 July 1994; 4 ♂, 2 ♀, 1 nymph, pond Jim Jim Creek, at Jim Jim campground, Kakadu National Park, 23 July 1994; 1 ♀, pool Twin Falls, Kakadu National Park, 23 July 1994; 1 ♀, Barramundie Creek, Kakadu National Park, 24 July 1994; 2 ♂, 5 ♀, 1 nymph, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 14 ♂, 1 ♀, 3 nymphs, plunge pool Gunlom Falls, Kakadu National Park, 25 July 1994; 1 ♂, Southern Rockhole, Katherine Gorge National Park, 27 July 1994; 11 ♂, 9 ♀, 1 nymph, Lily Ponds Falls, Katherine Gorge National

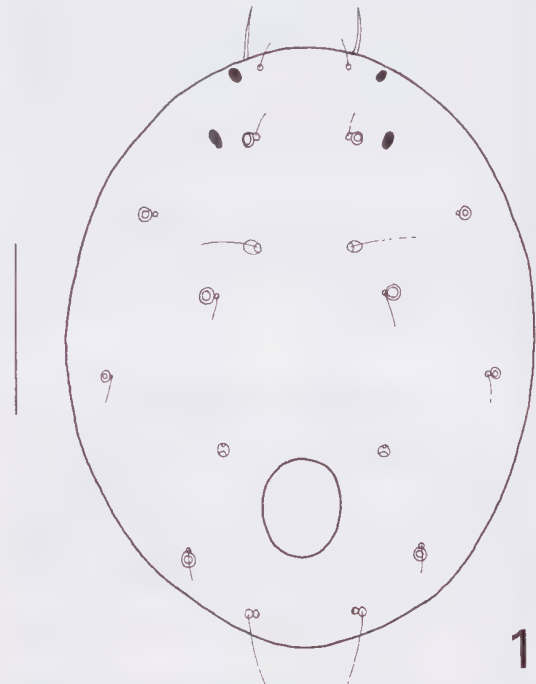


Figure 1 *Limnesia parasolida* K.O. Viets: 1, dorsal view, ♂. Scale line = 200 µm.

Park, 27 July 1994; 9 ♂, 6 ♀, 1 nymph, small stream, Butterfly Gorge, Katherine Gorge National Park, 27 July 1994; 2 ♂, 1 ♀, 1 nymph, Katherine River, near visitor's center, Katherine Gorge National Park, 28 July 1994; 1 ♀, pond Chinaman Creek, 16 km south of Katherine, 29 July 1994; 6 ♂, 7 ♀, 1 nymph, plunge pool Edith Falls, Katherine Gorge National Park, 30 July 1994; 3 ♂, 1 ♀, Douglas River, at Douglas Hot Springs, 1 August 1994; 1 ♂, 1 ♀, ponds Ormiston Gorge, Ormiston Gorge National Park, 6 August 1994; 3 ♂, waterhole Ormiston Gorge, Ormiston National Park, 6 August 1994.

Western Australia: 8 ♂, 26 ♀, 3 nymphs, Fortescue Falls (pool), Hamersley Range National Park, 11 August 1994; 5 ♂, 12 ♀, 12 nymphs, pond Dales Gorge, Hamersley Range National Park, 12 August 1994; 14 ♂, 12 ♀, 5 nymphs, pond Kalamina Gorge, near falls, Hamersley Range National Park, 13 August 1994; 2 ♂, streams originating in Chinderwariner Pool, Millstream-Chichester National Park, 15 August 1994; 4 nymphs, Palm Pool, Millstream-Chichester National Park, 15 August 1994; 2 nymphs, Deep Reach Pool, Millstream-Chichester National Park, 15 August 1994; 2 nymphs, western part Deep Reach Pool, Millstream-Chichester National Park, 16 August 1994; 2 ♂, 2 ♀, Python Pool, Millstream-Chichester National Park, 17 August 1994; 5 ♂, 1 ♀, Jones River, east of Roeburne, 17 August 1994; 3 ♂, 2 ♀, 2 nymphs, Fortescue River, at crossing with North West Coastal Highway, 18 August 1994; 2 ♂, Ashburton River, at crossing with North West Coastal Highway, 18 August 1994.

Remarks

In some populations, males and females possessing an aberrant number of acetabula, co-occur with specimens having the normal two pairs of three acetabula. The following aberrant numbers of acetabula have been recorded (males as well as females): 2+2, 2+3, 7+7 and 8+8. All these specimens are otherwise similar to *L. parasolida*, so I assigned them to that species. The number of acetabula is used for subgeneric splitting within the genus *Limnesia*, e.g. tetracetabulate species are assigned to *Tetralimnesia*. It is clear that the number of acetabula cannot be used for subgeneric splitting. Cook (1974) has pointed out the likelihood that unrelated species are lumped in subgenera of *Limnesia*.

Occasionally, the IV-leg-5 of *L. parasolida* has two stiff swimming setae. Cook (1986) mentioned the occurrence of only one stiff setae on this leg segment.

L. parasolida shows large variation in length. Females range from 320 to 1344 in length, the lower value belonging to a young female. Males ranged from 523 to 912. Cook (1986) gives the following

measurements: females 638–850, males 760–896. Small specimens usually have a short terminal seta on IV-leg-6, 77–84 in length. In larger specimens this seta measures 127–137. However, intermediate lengths do occur. It might be possible that more than one species is present, but morphological characters do not allow a separation.

Distribution

Previously reported from Northern Territory (Alice Springs area) (K.O. Viets, 1984) and Queensland (Cook, 1986; Smit, 1992). With the new records, it can be concluded that *L. parasolida* is a common species of the northern half of Australia.

Limnesia (Limnesia) rubra sp. nov.

Figures 2–4

Material Examined

Holotype

♂, plunge pool Edith Falls, Katherine Gorge National Park, Northern Territory, Australia, 30 July 1994 (NTM).

Paratypes

1 ♂, 1 ♀ (ZMA), 1 ♀ (NTM), same data as holotype.

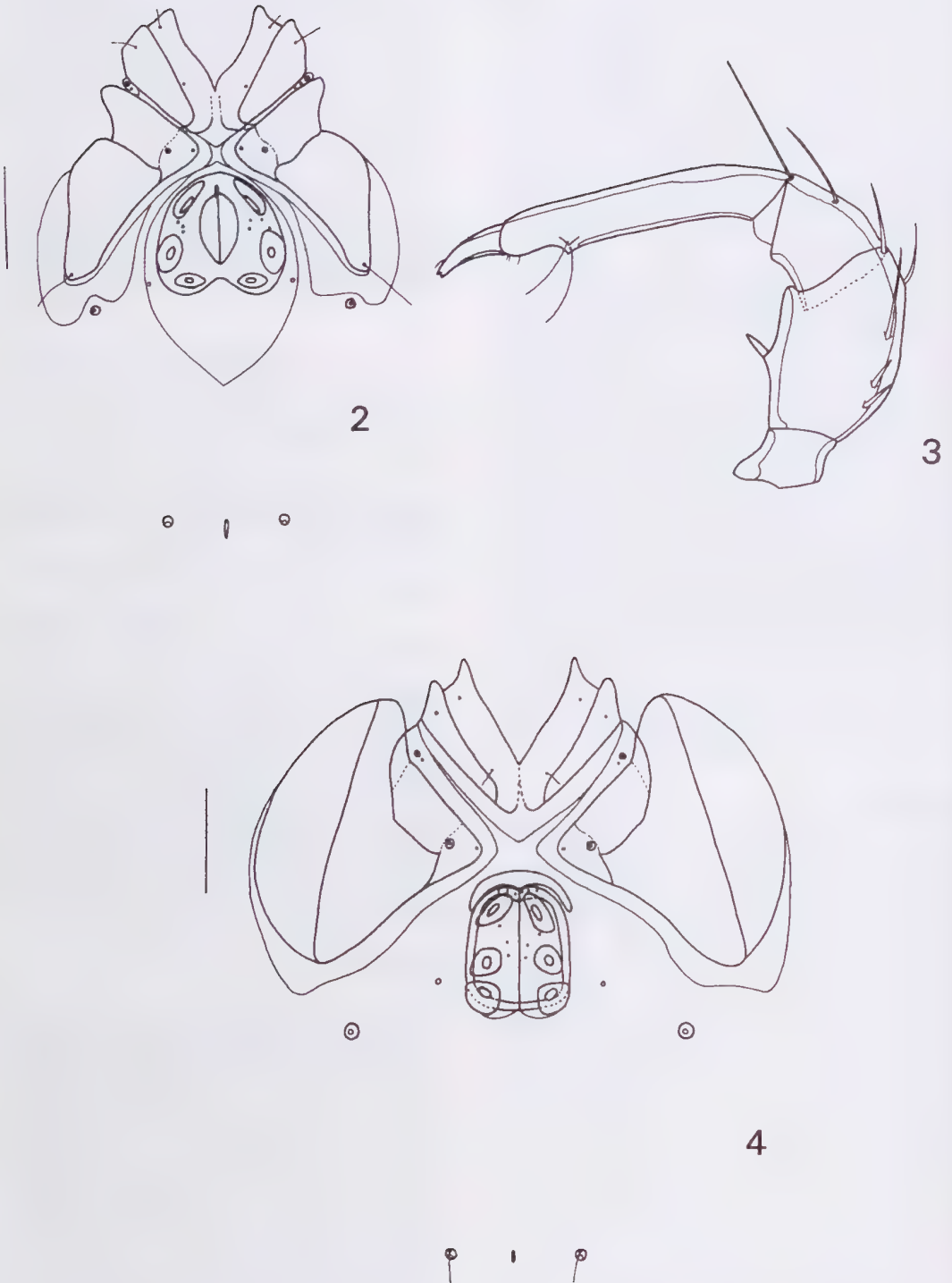
Diagnosis

Male acetabular plates forming a complete ring surrounding the gonopore, extensive secondary sclerotization around fourth coxal plates and genital field, first coxal plates fused medially, capitular bay deep, Glandula *Limnesiae* on third coxal plates and well separated from associated setae, peg-like seta on ventral margin of PII not on a tubercle, legs with swimming setae, chitinized parts coloured red.

Description

Male

Body 1067 (989) long and 902 (873) wide; chitinized parts coloured red. Integument smooth. Dorsum with an elongated platelet, 136 (136) in length. Capitular bay deep, longer than medial margins of first coxal plates. First coxal plates fused medially. Glandula *Limnesiae* on third coxal plates, well separated from the associated setae. Extensive secondary sclerotization around fourth coxal plates and genital field, and to a lesser extent medial of third coxal plates and posterior of first coxal plates. Gonopore 136 (120) long, completely surrounded by acetabular plates. Genital field with two pairs of three acetabula, the most anterior pair elongated. Excretory pore between associated glandularia. Lengths of PI-PV: 29, 144, 91, 206, 60.



Figures 2–4 *Limnesia rubra* sp. nov., holotype ♂: 2, ventral view; 3, palp ♂; paratype ♀: 4, ventral view. Scale lines: 2, 4 = 200 μm ; 3 = 100 μm .

Peg-like seta of ventral margin of PII not on a tubercle; setal tubercles of PIV small. Lengths of I-leg-4-6: 142, 166, 132. Lengths of IV-leg-4-6: 216, 233, 214; distal seta of IV-leg-6 142 long. III-leg-4 with one, III-leg-5 with nine, IV-leg-4 with four and IV-leg-5 with two long swimming setae.

Female

Body 1212–1397 long and 1018–1096 wide. Dorsum with an elongated platelet, 184–213 long. First coxal plates fused medially. A strip of secondary sclerotization along coxal plates. Gonopore 194 long. Genital field with two pairs of three acetabula. A genital sclerite 204 in width, anterior of genital field. Excretory pore between associated glandularia. Palp as in male; lengths of PI-PV: 36, 146, 118, 233, 34. Lengths of I-leg-4-6: 166, 194, 156. Lengths of IV-leg-4-6: 242, 272, 252; length of distal seta of IV-leg-6 146. III-leg-4 with one, III-leg-5 with eight, IV-leg-4 with four and IV-leg-5 with three long swimming setae.

Remarks

The new species belongs to the *solida*-group (*L. australica* Lundblad, *L. parasolida*, *L. solida*) of Cook (1986). The only other species of that group with the Glandula Limnesiae well separated from the associated setae, *L. parasolida*, has the gonopore as large as the genital field and less extensive secondary sclerotization. Further, *L. rubra* has long swimming setae (as in *australica*), while *parasolida* and *solida* have stiff swimming setae. The combination of long swimming setae and well separated Glandula Limnesiae and associated setae will separate the female from other females of the *solida*-group.

Etymology

Named for its conspicuous red colour.

Limnesia (Limnesia) solida Lundblad

Figure 5

Limnesia solida Lundblad, 1947: 46; K.O. Viets, 1975: 93; Smit, 1992: 95.

Material Examined

Australia: Northern Territory: 1 ♂, Home Billabong, Kakadu National Park, 22 July 1994; 1 ♀, Jim Jim Billabong, at crossing with Kakadu Highway, Kakadu National Park, 22 July 1994; 2 ♂, pond Jim Jim Creek, at Jim Jim campground, Kakadu National Park, 23 July 1994; 2 ♂, pools upstream of Waterfall Creek, Kakadu National Park, 25 July 1994; 1 ♂, 3 ♀, Kambolgie Creek, Kakadu National Park, 26 July 1994; 1 ♀, Southern Rockhole, Katherine Gorge National Park, 27 July 1994; 4 ♂, 3 ♀, 1 nymph, billabong near Douglas Hot Springs, 1 August 1994; 6 ♂, 14 ♀, 1 nymph,

waterhole Kantju Gorge, Ayers Rock, 4 August 1994; 1 ♀, ponds Ormiston Gorge, Ormiston Gorge National Park, 6 August 1994.

Western Australia: 7 ♂, 9 ♀, 1 nymph, Fortescue Falls (pool), Hamersley Range National Park, 11 August 1994; 2 ♂, 7 ♀, 5 nymphs, Circular Pool, Hamersley Range National Park, 12 August 1994; 1 ♀, pond Dales Gorge, Hamersley Range National Park, 12 August 1994; 3 ♂, 2 ♀, 1 nymph, pond Knox Gorge, Hamersley Range National Park, 13 August 1994; 9 ♂, 17 ♀, 1 nymph, pool Joffre Gorge, Hamersley Range National Park, 13 August 1994; 11 ♂, 5 ♀, 2 nymphs, pond Kalamina Gorge, near falls, Hamersley Range National Park, 13 August 1994; 2 ♀, Handrail pool, Weena Gorge, Hamersley Range National Park, 14 August 1994; 10 ♂, 15 ♀, pond Hancock Gorge, Hamersley Range National Park, 14 August 1994; 8 ♂, 6 ♀, 3 nymphs, Palm Pool, Millstream-Chichester National Park, 15 August 1994; 2 ♀, 1 nymph, small pond near Crossing Pool, Millstream-Chichester National Park, 16 August 1994; 1 ♀, Crossing Pool, Millstream-Chichester National Park, 16 August 1994; 11 ♂, 4 ♀, Python Pool, Millstream-Chichester National Park, 17 August 1994; 18 ♂, 27 ♀, 1 nymph, McKenzie Spring, Millstream-Chichester National Park, 17 August 1994; 14 ♂, 6 ♀, pond Snake Creek, Millstream-Chichester National Park, 17 August 1994; 5 ♂, 4 ♀, 1 nymph, Jones River, east of Roeburne, 17 August 1994; 1 ♂, 1 ♀, 2 nymphs, Fortescue River, at crossing with North West Coastal Highway, 18 August 1994; 1 ♂, 17 ♀, Ashburton River, at

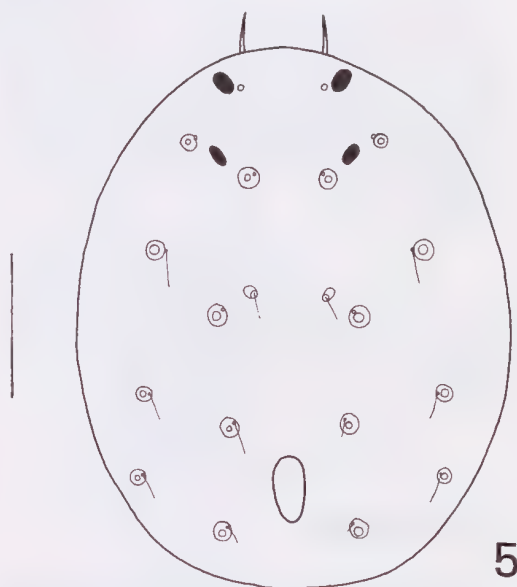


Figure 5 *Limnesia solida* Lundblad, dorsal view, ♂. Scale line = 200 µm.

crossing with North West Coastal Highway, 18 August 1994.

Remarks

According to Cook (1986) *L. solida* and *L. parasolida* differ in the number of stiff swimming setae on IV-leg-5 (*solida* with two setae and *parasolida* with one). However, the number of stiff setae on IV-leg-5 varies in both species from 1–2, and can therefore not be used to separate the two species. The two species are easily separated by the platelet on the dorsum, which is larger and more rounded in *L. parasolida* (Figure 1), and the distance between the Glandula Limnesiae and the associated seta (large in *parasolida*, short in *solida*). In contradiction to Smit (1992), the male does have a platelet on the dorsal shield (Figure 5), 68–86 long. Males of *L. parasolida* have the gonopore as long as the genital field, in *L. solida* the gonopore is distinctly shorter than the genital field.

The seta associated with coxoglandularia 2 of *L. solida* are not always closer to the genital field (as stated by Cook), but occasionally halfway between the genital field and the coxoglandularia 2. Males of *solida* sometimes show some secondary sclerotization posterior of the genital field and fourth coxal plates. Males of this study are 737–941 in length, the long seta of IV-leg-6 measured 62–98 in length. Females measured 902–1260 in length. The nymphs of the two species can be separated with the platelet on the dorsal shield, which is 17–33 long in *L. solida* and 48–70 in *L. parasolida*.

Distribution

A widespread species in Australia, previously reported from Victoria (only one record, the holotype) and Queensland (K.O. Viets, 1975; Smit, 1992). The species is much more common in the Northern Territory and Western Australia compared to Queensland and Victoria. So far, no records are known from the southwestern part of Western Australia.

Genus *Physolimnesia* Halík

Centrolimnesia (*Physolimnesia*) Halík, 1940: 21.

Physolimnesia Halík: Lundblad, 1941b: 365.

Physolimnesia katherine sp. nov.

Figures 6–10

Material Examined

Holotype

♂, Southern Rockhole, Katherine Gorge National Park, Northern Territory, Australia, 27 July 1994 (NTM).

Paratypes

3 ♂, 2 ♀ (NTM), 2 ♂, 2 ♀ (WAM), 2 ♂, 2 ♀, 1 nymph (ZMA), same data as holotype.

Diagnosis

Male and female with four pairs of large acetabula, gonopore much shorter than length of genital field; third and fourth legs of male modified. Seta on ventral margin of second palp segment on a tubercle; fourth palp segment with distinct setal tubercles.

Description

Male

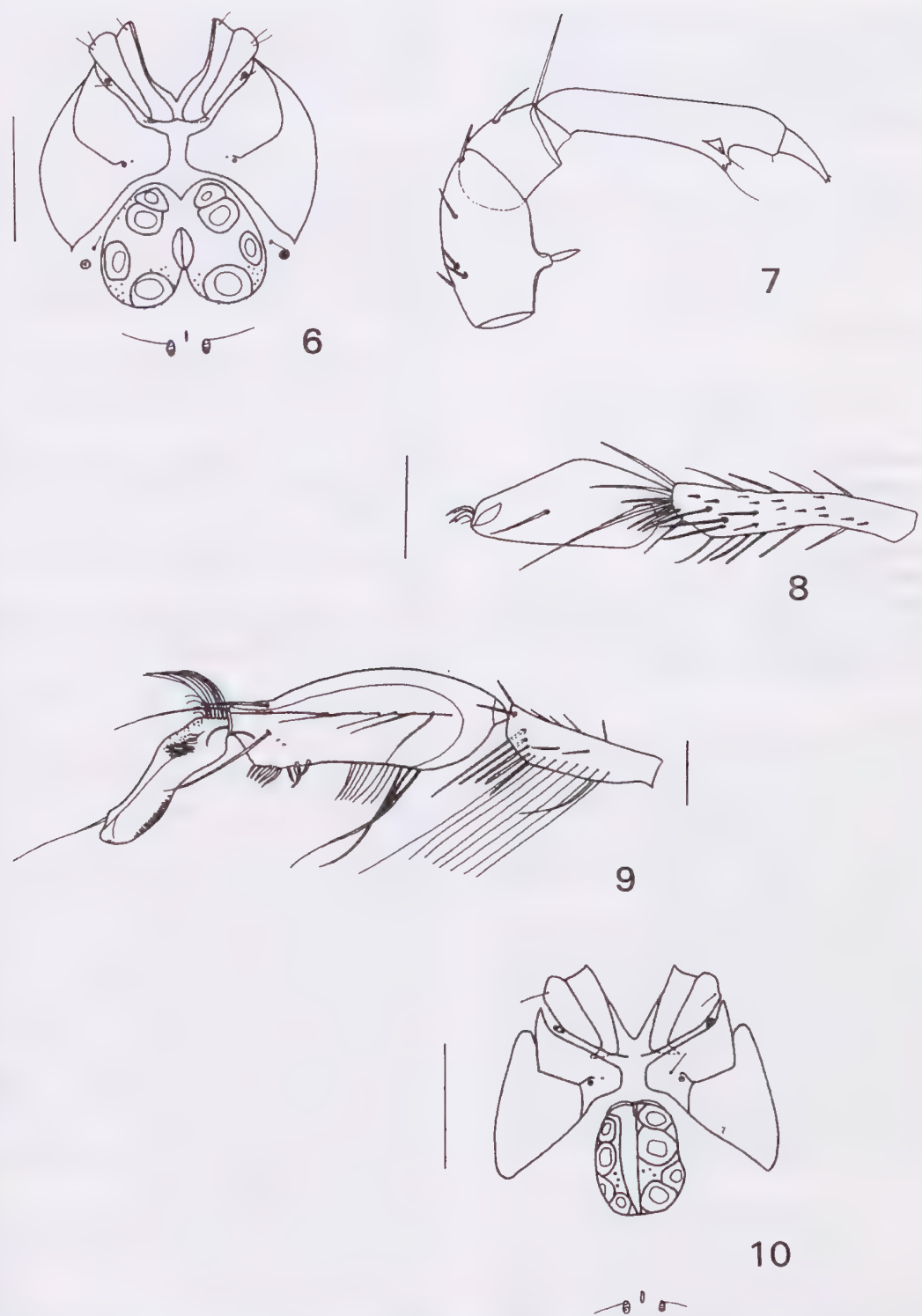
Body 776 (630–863) long and 562 (495–592) wide. Dorsal platelets absent. First coxal plates not fused medially, but secondary sclerotization present between first coxal plates. Glandula Limnesiae medial of suture line of third and fourth coxal plates; associated setae close to Glandula Limnesiae. Genital field with four pairs of large acetabula. Gonopore 77 long, much shorter than genital field. Excretory pore between associated glandularia. Measurements of PI-PV: 19, 125, 89, 175, 50. Seta on ventral margin of PII on a tubercle, seta longer than tubercle. Ventral margin of PIV with distinct setal tubercles. Third and fourth legs modified. III-leg-6 expanded and flattened, with one seta on medial side. IV-leg-5 large, with three long, thick setae and eight short, fine setae on ventral margin, a row of hyaline setae on anteroventral margin, 11 (11–14) setae on medial side and three long setae on anterior part of segment; distal margin with one curved seta. IV-leg-6 ventrally with a row of grooves, anterodorsal margin with a group of curved setae, a group of fine setae on medial side and anteroposteriorly with a 161 long seta. Measurements of first, third and fourth legs: I-leg-4-6: 154, 146, 144, I-leg-6 with an undulating ventral margin. III-leg-4-6: 240, 236, 199. IV-leg-4-6: 228, 388, 248. Second, third and fourth legs with swimming setae.

Female

Body 553–1018 long and 456–795 wide. Dorsal platelets absent. Position of Glandula Limnesiae as in male. Genital field with two pairs of four, large acetabula. Palp as in male. Measurements of PI-PV: 22, 125, 60, 173, 53. Measurements of I-leg-4-6: 115, 125, 120. Measurements of IV-leg-4-6: 211, 223, 218; IV-leg-6 with a 132 long seta. Third and fourth legs with swimming setae.

Remarks

Now that the second *Physolimnesia* species is known, the diagnosis of the genus has to be altered: genital field with three or four pairs of acetabula. The new species differs from



Figures 6–10 *Physolimnesia katherine* sp. nov., paratype ♂: 6, ventral view; holotype ♂: 7, palp; 8, III-leg-5-6; 9, IV-leg-4-6; paratype ♀: 10, ventral view. Scale lines: 6, 10 = 200 µm; 7, 8, 9 = 100 µm.

Physolimnesia australis (Halík) in having four pairs of large acetabula (three in *P. australis*), and a more slender III-leg-6 of the male. The row of 11–14 seta on the medial side of IV-leg-5 is absent in *australis*, but in general the modified third and fourth legs of the two species are remarkably similar.

Etymology

Named after the Katherine River, which is near the type locality; the name is a noun in apposition.

Genus *Timmsilimnesia* K.O. Viets

Timmsilimnesia K.O. Viets, 1984: 422.

Timmsilimnesia inga (K.O. Viets), new combination

Limnesia inga K.O. Viets, 1975: 94.

Timmsilimnesia prehensens K.O. Viets, 1984: 422.

New synonymy.

Material Examined

Australia: Northern Territory: 1 ♀, 1 nymph, billabong Nourlangie Creek, Kakadu National Park, 20 July 1994; 9 ♂, 5 ♀, small billabong, Gunlon, Kakadu National Park, 25 July 1994; 1 ♀, 5 nymphs, Manton Dam, 1 August 1994.

Remarks

Cook (1986) was the first to recognise that the two species were morphologically similar, although he did not synonymize the two species. Now that males of *Timmsilimnesia prehensens* and females of *Limnesia inga* are collected on the same location, it is clear that they are conspecific. Therefore, the new name of the species must be *Timmsilimnesia inga* (K.O. Viets).

Both male and female were hitherto only known from holotypes each based on one sex, collected in Northern Territory and Queensland respectively. The males from this study measure 1200–1464 in length and 996–1284 in width, the females measure 1236–2280 in length and 1080–1944 in width. No length and width were given by K.O. Viets (1984) for the male, the females are much larger than the holotype female from Queensland. The colour of the chitinized parts is not red, as reported by K.O. Viets (1975), but yellow.

ACKNOWLEDGEMENTS

I am indebted to Dr M.S. Harvey for his help with the preparations for this trip, to the Western Australian Department of Conservation and Land Management (Como), the Australian National Parks and Wildlife Service (Darwin) and the Conservation Commission of the Northern

Territory (Palmerston) for their permission to collect water mites in the national parks of Western Australia and Northern Territory and to G.M. van der Pal for her assistance with the fieldwork.

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Manuscript received 19 February 1997; accepted 24 July 1997.

Dicranodromia karubar Guinot, 1993, a deep-water crab new to the Australian fauna (Crustacea: Brachyura: Homolodromiidae)

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INTRODUCTION

Of the eight species of *Dicranodromia* A. Milne Edwards, 1880 occurring in the Indo-West Pacific ocean, only one is known from Australian waters (Davie & Short, 1989; Guinot, 1995). Because the two homolodromiid specimens (a male and an ovigerous female from Queensland, from depths of 590 m and 650 m, respectively) known from Australia are damaged (Guinot, 1995: 220), their identity is still unclear. Davie and Short (1989: 158–159) referred the male QM W10801 to *D. baffini* (Alcock and Anderson, 1899), whereas Guinot (1995) assigned it, as well as the ovigerous female QM W14372, to *Dicranodromia* aff. *foersteri* Guinot, 1993, "sous réserve".

Among the crab material in the collections of the Western Australian Museum, Perth, is an ovigerous female of *Dicranodromia karubar* Guinot, 1993. This species was previously known from Indonesia, and is here recorded for the first time from Australian waters.

The terminology follows Guinot (1995). Abbreviations used include: QM = Queensland Museum, Brisbane; WAM = Western Australian Museum, Perth; P1, cheliped; P2–P5, second, third, fourth and fifth pereopod respectively; cl and cw correspond to carapace maximal length and width respectively expressed in millimeters (mm); m, meters.

Dicranodromia karubar Guinot, 1993

Figure 1A–E

Dicranodromia karubar Guinot, 1993: 1228, figure 4; 1995: 213, figure 15a–c, 16A–D, 25A–B

Material examined

Australia, Western Australia, west of Lacepede Archipelago, F. V. "Soela", 21.2.1984, 16°54.1'S – 119°56.6'E to 16°35.2'S – 119°53.1'E, 434 m: ovigerous female cl 29; cw 24 (WAM 166–93).

Geographic and bathymetric range.— Indonesia; Moluccas Archipelago (Kai and Tanimbar islands); and Western Australia (this report); from 356 to 468 m.

Remarks

The Western Australian specimen agrees well with the Indonesian specimens. In the Australian material the dactylus of P2 and P3 bears 6–8 sharp spines on the cutting edge (figure 1E), and although this was not described by Guinot (1995: 202 in the key; 215), it also occurs in the Indonesian specimens (Guinot, *in letteris*).

D. karubar can be distinguished from *D. foersteri* and *D. baffini* by the following characters: (1) in *D. karubar* the carapace is covered with short, thick, erect, yellowish tomentum, whereas *D. foersteri* has scattered setae; (2) the rostral median spine is absent or represented by a tubercle in *D. karubar*, but represented by a spine in *D. foersteri*; (3) the palm of the cheliped is adorned with few and scattered granules (figure 1B) in *D. karubar*, but regularly covered with granules in *D. foersteri*; (4) there is a distinct comma-like bulge located just above the opening of the spermatheca in *D. karubar*, but only a rounded tubercle in *D. foersteri*. Characters 3 and 4 also distinguish *D. karubar* from *D. baffini* (Guinot, 1995: 217, 220).

The Australian specimen of *D. karubar* carried about 80 reddish eggs of 1 mm diameter. Guinot (1995: 166) noticed that "...à taille sensiblement égale des individus, il existe selon les espèces des différences assez grandes dans le diamètre des oeufs, et donc dans leur nombre". Caustier (1895) mentioned eggs of 2 mm diameter in *D. ovata* A. Milne Edwards, 1880; Martin (1991) examined an ovigerous female of *D. felderi* Martin, 1990, carrying oval eggs of 2.4 × 1.9 mm; Guinot (1995) found relatively large and few eggs in the following species: *D. pequegnati* Guinot, 1995, about 30 eggs of 2 × 1.5 mm; *D. spinulata* Guinot, 1995: apparently no more than six eggs measuring about 1 mm; *D. doederleini* Ortmann, 1892: less than 50 large eggs; *D. foersteri*: 150–200 subspherical eggs ranging from 2 to 2.2 mm.

ACKNOWLEDGEMENTS

I am sincerely grateful to Danièle Guinot (Muséum national d'Histoire naturelle, Paris), to

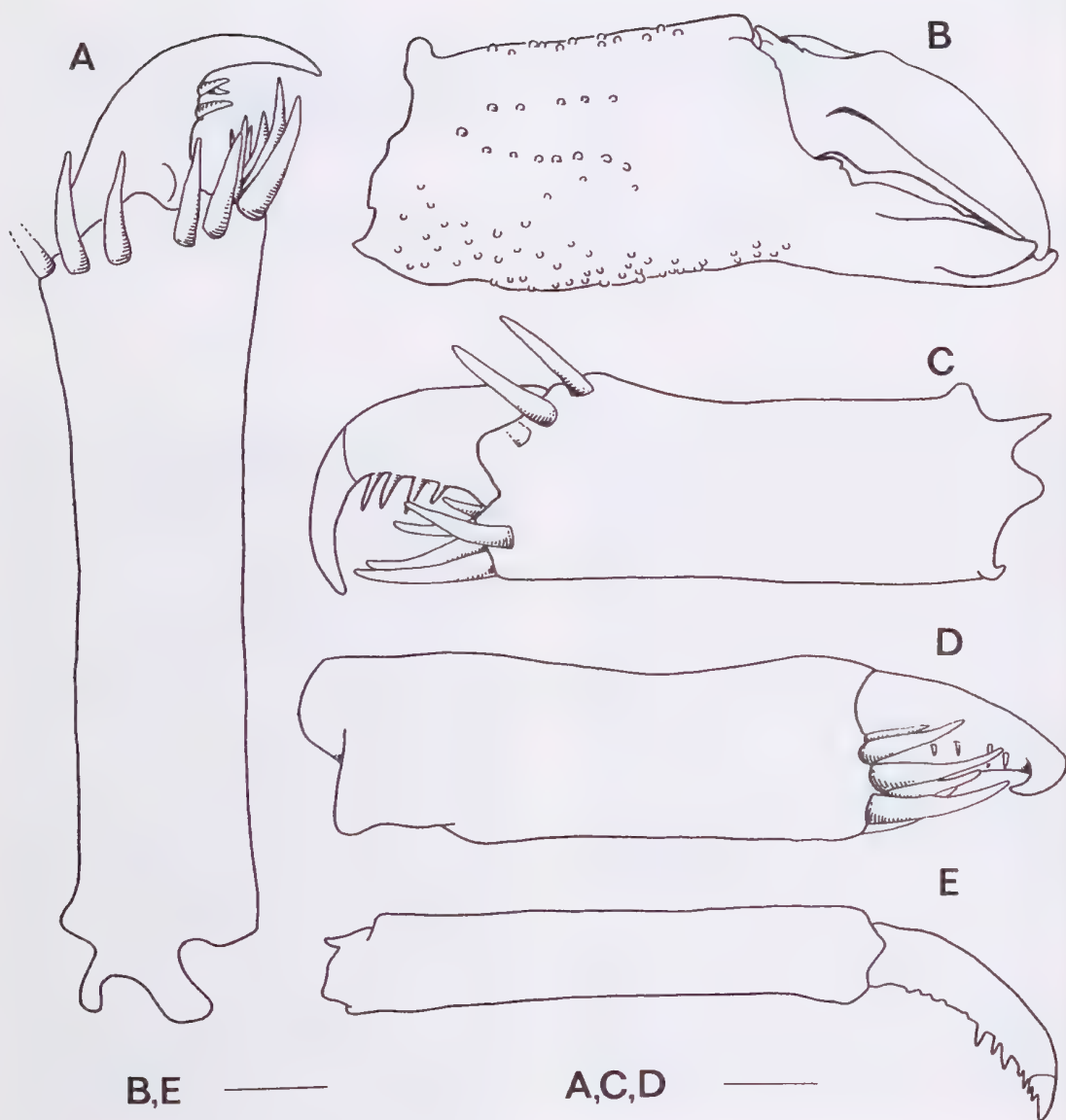


Figure 1 Dactylus and propodus of left cheliped and left pereiopods 2, 4, 5 in *Dicranodromia karubar* Guinot, 1993, western Australia, 434 m: ovigerous female cl 29; cw 24 (WAM 166-93). **A**, external view of fifth pereiopod (P5). **B**, palm and movable finger of cheliped. **C**, external view of fourth pereiopod (P4). **D**, ventral view of fourth pereiopod. **E**, internal view of second pereiopod. Notice that propodus is much longer in P5 than in P4. Scales: B, E = 5 mm; A, C, D = 2 mm.

Peter J. F. Davie (QM) and to Diana S. Jones (WAM) for reviewing a draft of the manuscript. Peter also kindly checked the English text. I also thank Valéria G. Veloso (Universidade do Rio de Janeiro) for calling my attention to this interesting specimen and Diana for making it available for

study. Drawings are by Georgia M. de O. Franco. Support of studies on the systematics of Decapoda by CNPq (National Council for the Development of Science and Technology, Brasília) in the form of ongoing grant 520254/95-3 is gratefully acknowledged.

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Manuscript received 22 April 1997; accepted 29 August 1997.

Azooxanthellate Scleractinia (Cnidaria: Anthozoa) of Western Australia

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Abstract – One hundred five species of azooxanthellate Scleractinia are known from Western Australia. Seventy of these species are reported herein as new records for Western Australia, 57 of which are also new to Australia. Eleven new species are described. The study was based on an examination of approximately 1725 specimens from 333 stations, which resulted in additional records of 98 of the 105 known species. New material was examined from six museums, as well as the historical material of Folkesson (1919) deposited at the Swedish Museum of Natural History.

A majority (69/105 species) of the azooxanthellate species known from Western Australia occur in the tropical region of the Northern Australian Tropical Province (bordered to the south by the Houtman Abrolhos Islands and Port Gregory), which can be considered as a southern extension of the larger Indo-West Pacific tropical realm. Nine species are endemic to this region, and the highest latitudinal attrition of species occurs between Cape Jaubert and the Dampier Archipelago. Another 20 species, also known from tropical regions, extend to varying degrees into the Southern Australian Warm Temperate Province. Twelve species are restricted to warm temperate waters of the Southern Australian Warm Temperate Region, most of these species being relatively shallow in depth distribution. A majority of species (53) occur at depths shallower than 200 m, 46 occur exclusively deeper than 200 m (to 1011 m), and 6 species cross the 200 m isobath.

Commensal relationships (galls) with ascothoracidan crustaceans were found with two corals hosts (*Madrepora oculata* and *Deltocyathus magnificus*), and with acrothoracican cirripedes (thecal borings) with six coral hosts: *Flabellum politum*, *Truncatoflabellum folksoni*, *T. formosum*, *T. australiensis*, *Javania lamprotichum*, and *Dendrophyllia alcocki*.

INTRODUCTION

Veron and Marsh (1988) listed 318 species of "hermatypic" (or zooxanthellate) Scleractinia from Western Australia. The term zooxanthellate simply means that the coral lives in symbiosis with dinoflagellate algae and thus must occur within the euphotic zone and in tropical to subtropical temperatures, and usually implies that the coral contributes to reef structure, although not necessarily (Schuhmacher and Zibrowius 1985). There is, however, a second ecological class of Scleractinia known as azooxanthellate corals, literally those species that do not live symbiotically with dinoflagellate algae. These species are not limited to the euphotic zone or by warm temperatures and are ubiquitous, known from the Norwegian Sea to Antarctica from the intertidal to 6328 m (Cairns and Stanley 1982). Coralla of azooxanthellate species are usually small, solitary, and do not contribute to reef structure, but exceptions to all these conditions occur. Approximately equal numbers of both types of coral species occur in the world oceans. 105 species of azooxanthellate corals occur off the entire coast of

Western Australia, ranging from the intertidal to 1011 m. These, combined with the known zooxanthellate coral fauna, result in a total of 422 scleractinian species from Western Australia, one species, *Heteropsammia cochlea*, occurring in both forms.

The history of the azooxanthellate coral fauna of Western Australia is not lengthy. Only 13 publications report 35 azooxanthellate species from this region, the first (Rehberg, 1892) being *Heterocyathus pulchellus* from the "Westkuste Australiens", a species later synonymized with *H. sulcatus* (Verrill, 1866) by Hoeksema and Best (1991).

Ten new records were added by Folkesson (1919), resulting from collections made by E. Mjöberg's Swedish Scientific Expeditions to Australia (1910–1913). These records, which include three new species and one new genus, were from WSW of Cape Jaubert and off Broome at depths of 11–42 m, and include: *Truncatoflabellum spheniscus* (originally reported as *Flabellum rubrum*, in part); *T. aculeatum* (reported as *F. rubrum*, in part); *T. angiosomum*; *Placotrochus laevis*; *Heterocyathus aequicostatus*; *H. alternatus*; *H. hemisphericus* (reported as

Spongiocyathus typicus); *Rhizosmilia multipalifera* (reported as *Paracyathus porphyreus*); *Conocyathus gracilis* (reported as *Trematotrochus zelandiae*); and *Leptopsammia columna* (Figs 9f, i). An eleventh species, *Paracyathus profundus* Duncan, 1889, was reported, but this specimen is not preserved well enough to verify its identification. Folkesson's specimens are deposited at the Swedish Museum of Natural History, Stockholm.

In a paper reporting deep-water corals from South Australia, Victoria, Tasmania, and New South Wales, Hoffmeister (1933) also reported one species, *Flabellum tuthilli*, from the continental slope of the Great Australian Bight off Western Australia.

The Miocene fossil species *Trematotrochus lateropenus* Dennant, 1899 was reported by Wells (1942) from Langley Park Bore, Perth. As noted in the species account, this fossil may be *Trematotrochus verconis* Dennant, 1904.

In his book on Australian and Indo-Pacific reef corals, Veron (1986) also included a short chapter (pp. 597–610) on Australian azooxanthellates. Although exact localities and specific identifications are sometimes wanting, eight records of Western Australian azooxanthellate corals can be extracted from this book, including the following six new records: *Deltocyathus magnificus* (reported as *Fungiacyathus*); *Cyathelia axillaris*; *Trochocyathus apertus* (reported as *Premocyathus ? compressus*); *Endopachys grayi* (reported as *Endopachys* sp.); *Heteropsammia cochlea*; and *Tubastraea coccinea* (reported as *T. aurea*). Additional Western Australian records of *Heteropsammia cochlea* can also be found in Veron and Marsh (1988) and Veron (1993).

Grygier (1991) reported two Western Australian azooxanthellate species as hosts for petraracid ascothoracid Crustacea, one of the species, *Flabellum magnificum*, being a new record for this state, the other being *Deltocyathus magnificus*. In the same context, Grygier and Cairns (1996) reported Western Australian *Madrepora oculata* as hosts for these parasites.

In a paper reviewing the Scleractinia of southeastern Australia, Cairns and Parker (1992) also included 13 new records from the southern coast of Western Australia: *Culicia australiensis*, *C. hoffmeisteri*, *Anthemiphyllia dentata*, *Desmophyllum dianthus* (reported as *D. cristagalli*), *Solenosmilia variabilis*, *Conotrochus funiculocolumna* (reported as *Conotrochus brunneus*), *Trematotrochus alternans*, *Platytrachus laevigatus*, *P. hastatus*, *Australocyathus vincentinus*, *Rhizotrochus tuberculatus*, *Notophyllia recta*, and *N. piscacauda* (reported as *Notophyllia* n. sp.). These specimens were collected by the *Soela*, *R/V Comet*, *Adelaide Pearl*, and *BANZARE*, and from the *Verco* and *WAM* collections; they are deposited at the South Australian Museum, Western Australian Museum, and NMNH.

An additional record of *Rhizotrochus tuberculatus* from the Late Pleistocene of Cape Burney, southwestern Western Australia was reported by Johnson, Baarli, and Scott (1995).

Finally, Cairns (1995) reported *Conocyathus zelandiae* from King George Sound, and Cairns and Zibrowius (1997) reported three species from the northeastern tip of Western Australia, one of them, *Balanophyllia imperialis*, being a new record for the state.

MATERIAL AND METHODS

Museum Abbreviations:

AMS	Australian Museum, Sydney.
BMNH	British Museum (Natural History), London.
NTM	Museum & Art Gallery of the Northern Territory, Darwin.
NMNH	National Museum of Natural History, Smithsonian, Washington, D. C.
NMV	National Museum of Victoria, Melbourne.
SAM	South Australian Museum, Adelaide.
SMNH	Swedish Museum of Natural History, Stockholm.
USNM	United States National Museum (now the National Museum of Natural History).
WAM	Western Australian Museum, Perth.

Expedition Abbreviations:

DEKI	Danish Expedition to the Kei Islands (1922).
KARUBAR	French-Indonesian expedition (1991) that collected in the southeastern Banda Sea. Named for the Kai, Aru, and Tanimbar Islands.

Morphological Terms Abbreviations:

GCD	Greater Calicular Diameter
GCD:H	Ratio of greater calicular diameter to corallum height
GCD:LCD	Ratio of greater to lesser calicular diameter
H:D	Ratio of height to corallum diameter
PD:GCD	Ratio of pedicel diameter to greater calicular diameter
Sx, Cx, Px	Septa, costae, or pali (respectively) of cycle designated by numerical subscript
Sx > Sy	Septa of cycle x wider than those of cycle y
SCI	Septal Concavity Index: ratio of distance from thecal edge to point of greatest septal inflection to length of thecal face measured along that septum
SSI	Septal Sinuosity Index: ratio of amplitude of lower inner edge of a septum to the thickness of that septum

Table 1 Distribution of the Western Australian Azooxanthellate Scleractinia (∧ no new material; * new to WA; ** new to Australia)

	AUSTRALIA											Depth (m)	Distribution Pattern (See Table 2)
	Western Australia												
	1	2	3	4	5	6	7	8	9	10	11		
FUNGICIACYATHIDAE													
** <i>Fungiacyathus</i> (F.) <i>stephanus</i>	x	x		x					x		x	304-720 400-420	1B 2A
**F. (F.) <i>fragilis</i>				x								101-300	1B
*F. (F.) <i>paliferus</i>	x	x		x		x						348-350	1E
**F. (F.) <i>multicarinatus</i>				x								300-302	1C
**F. (B.) <i>variegatus</i>		x		x								302-400	1C
**F. (B.) <i>granulosus</i>		x		x									
MICRABACIIDAE													
* <i>Letepsammia formosissima</i>	x	x		x		x	x	x	x			302-500 201	2A -
** <i>L. fissilis</i>				x								390-696	1C
** <i>Rhombopsammia niphada</i>		x		x								260-433	1B
** <i>Stephanophyllia complicata</i>	x	x		x					x				
RHIZANGIIDAE													
<i>Culicia australiensis</i>	x			x		x		x				18-180 0-10	2A 3A
<i>C. hoffmeisteri</i>					x	x		x				46	3A
* <i>Astrangia atrata</i>					x	x	x	x				intertidal	1C
** <i>Oulangia stokesiana</i>		x	x	x									
OCULINIDAE													
<i>Madrepora oculata</i>	x	x		x					x	x		304-544 12-40	1A -
<i>Cyathelia axillaris</i>		x			x								
ANTHEMIPHYLLIIDAE													
<i>Anthemiphyllia dentata</i>	x	x	x	x		x		x	x			154-240	2A
CARYOPHYLLIIDAE													
** <i>Caryophyllia</i> (C.) <i>transversalis</i>		x		x								224-302	1C
**C. (C.) <i>rugosa</i>	x	x		x				x				180-200	1B
**C. (C.) <i>quadrigenaria</i>		x		x				x				154-201	1C
**C. (C.) <i>stellula</i>	x				x							240-402	3B
**C. (C.) <i>atlantica</i>		x		x						x		298-530	1A
**C. (C.) <i>grandis</i>	x	x		x				x				394-596	1B
**C. (A.) <i>grayi</i>	x	x		x								130-150	1B
**C. (A.) <i>unicristata</i>		x		x								302-450	1C
**C. (A.) <i>decamera</i>		x		x								224-260	1C
** <i>Crispatotrochus rugosus</i>		x		x				x				296-298	1C
* <i>C. inornatus</i>				x			x					302-400	-
** <i>Oxymilia circularis</i>				x								201-404	1E
** <i>Trochocyathus philippinensis</i>		x		x								100-154	1C
* <i>T. apertus</i>		x	?	x								20-230	1C

The specimens on which this study was based originated primarily from the collections of the Western Australian Museum; however, additional Western Australian corals were studied from the NTM, SAM, NMV, AMS, and NMNH. In addition, the historical collection reported by Folkson (1919) was borrowed from the SMNH. Approximately 1725 specimens from 333 stations (many listed in Appendix) were used in the study. From this material, additional specimens of 98 of the 105 known Western Australian azooxanthellate species were obtained (Table 1). Seventy of the 105 species known from Western Australia are new records for the state (Table 1, * and **), 57 of which are new records for Australia (Table 1, **).

Synonymies are intended to be complete only for Australian records; otherwise, a reference is included that contains a description of the species and a fuller synonymy. Only new and previously poorly-known species are described and figured, as well as those that show unusual variation or are of doubtful identity. The scanning electron photomicrographs were taken by the author on an Hitachi S-570. In cases in which specimens lacked sufficient contrast for conventional photography, the corallum was stained with black cloth dye and coated with a thin layer of sublimed ammonium chloride.

A station list to all specimens reported follows the Reference section, except for localities listed as "other records" in the species accounts, which are given in full where listed.

ZOOGEOGRAPHY/DISTRIBUTION

Many authors (summarized in Wilson and Allen 1987; Morgan and Wells 1991) now recognize two marine biogeographic provinces for Western Australia: a Northern Australian Tropical Province and a Southern Australian Warm Temperate Province, with a broad overlap zone extending from North West Cape to as far south as Rottnest Island or even Cape Leeuwin. In a comprehensive analysis of shallow-water reef corals, Veron and Marsh (1988) and Veron (1995) suggested that the southern boundary of the tropical coral province extends to the Houtman Abrolhos Islands offshore but slightly more northerly on the mainland, i.e. Port Gregory. This cross shelf discrepancy is due to the offshore position of the warm, southward flowing Leeuwin Current and the coastal position of the colder, northward flowing Leeuwin Countercurrent (Hutchins 1994: 32). Veron (1993 and 1995) has shown that the number of reef corals dramatically drops from 201 at the Houtman Abrolhos Islands to 36 or less at and south of Port Gregory. It is acknowledged that many of the Western Australian azooxanthellate corals (which have a depth range of 0–1011 m, 46 of which are

found exclusively deeper than 200 m) are outside the influence of the Leeuwin Current are thus not subject to the same physical conditions as the inshore benthic fauna on which most zoogeographic conclusions have been based. And, according to Wilson and Allen (1987:43): "There is very little information available on the benthic fauna of the continental shelf and beyond". Nonetheless, the distributional patterns and affinities of azooxanthellate corals are remarkably similar to those of shallow-water faunas, as shown below. For the purpose of scoring Tables 1–2 and further zoogeographic discussion, the boundaries between the tropical and warm temperate provinces suggested by Veron and Marsh (1988) are used: the Houtman Abrolhos Islands (offshore) and Port Gregory (coastal).

Tropical West Australian Fauna.—As reviewed by Wilson and Allen (1987) and Morgan and Wells (1991), the northwestern coast of Western Australia is one of the southern extensions of the large Indo-West Pacific tropical realm. Of the 105 Western Australian azooxanthellate species, 87 (Table 1: column 4) are known from the Northern Australian Tropical Province, 69 (Table 2: patterns 1A–E) of which are considered to be restricted to tropical

Table 2 Categorization of Distribution Patterns and Number of Species among the Western Australian Azooxanthellate Scleractinia. Species characterizations listed in Table 1 (Four species not scored).

1. Species restricted to tropical regions (69 species):
 - A. Circumtropical in distribution or very widespread, including Indo-West Pacific and eastern Pacific and sometimes Atlantic Ocean: 6 species.
 - B. Found throughout tropical Indo-West Pacific, sometimes including the Ryukyu Islands, Kermadec and Norfolk Islands, Northern Territory and Queensland, and sometimes Hawaiian Islands: 23 species.
 - C. Found throughout Western Pacific: 29 species.
 - D. Amphi-Indian Ocean: 2 species.
 - E. Endemic to Western Australia (Northern Australian Tropical Province): 9 species.
2. Species that occur in tropical and warm temperate regions (20 species):
 - A. Species with a distribution beyond that of Western Australia: 19 species.
 - B. Endemic to western coast of Western Australia: 1 species.
3. Species endemic to temperate regions (12 species):
 - A. Temperate southern Australia only (Southern Australian Warm Temperate Province): 11 species.
 - B. Temperate southern Australia and South Africa: 1 species.

regions. These tropical species are subdivided into categories 1 A–E in Table 2, in order to show the extent of the distributions of these species in tropical areas beyond Western Australia. Nine species (9/87 = 10%), category 1E of Table 2, are endemic to this province, which is consistent with the degree of endemicity of other benthic invertebrates groups (i.e., molluscs, brachyuran decapods, echinoderms), summarized by Morgan and Wells (1991), as 10–17%. There is a general correlation between depth of occurrence and endemicity among the nine endemic species (Table 3: pattern 1E), 7 of the 9 endemic species (78%) being found at shallow depths (0–200 m), whereas only 48% (38/79 species of categories 1A–D, 2A of Table 3) of the more widespread tropical species are found at depths shallower than 200 m.

Another category of “tropical” species (patterns 2 A and B of Table 2) are those azooxanthellate species that occur both in tropical and temperate Western Australian regions, most of which occur not only in the tropical realm but also off warm temperate South Australia, Victoria, Tasmania, New South Wales, and/or Japan. Nineteen species have such distributions (Tables 1–2, pattern 2A), even though in some cases these species may not yet have been recorded from the tropical region of Western Australia (e.g., *Desmophyllum dianthus* and *Solenosmilia variabilis*) or the warm temperate region of Western Australia (e.g., *Paracontrochus zeidleri*, *Guynia annulata*, and *Flabellum hoffmeisteri*). In general, these species occur deeper than the exclusively tropical species (Table 3), 68% of the 19 species occurring exclusively deeper than 200 m. One species, *Rhizosmilia multilifera*, categorized as having pattern 2B, occurs from Cape Jaubert to 31°30'S latitude, and is thus far endemic to the western coast of Western Australia. Not surprisingly, it has a relatively shallow depth range.

As previously suggested, the number of tropical azooxanthellate species gradually attenuates with increasing southern latitude. Comprehensive numbers of species for various regions along the coast, such as those provided by Morgan and Wells (1991) for Crustacea, Veron and Marsh (1988) for corals, and Wells (1980) for molluscs, are not available for deep-water corals. To a certain degree our knowledge of the deep-water coral distributional ranges is a reflection of the regions and depths at which dredging vessels happened to make stations. Nonetheless, a preliminary tabulation can be given of the southern limit of the tropical species (Tables 2–3, categories 1 and 2) for which adequate data are available. For instance, of the species known from Western Australia, eight extend no farther south than the region defined by Browse, Scott, and Cartier Islands, 5 extend to Dampier Land, 5 to Rowley Shoals and Cape

Jaubert, 37 to the continental slope between Rowley Shoals and Port Hedland, 13 to Dampier Archipelago, 4 to the Cape Range/North West Cape region, 4 to Shark Bay, 5 to the Houtman Abrolhos Islands, 6 to Rottnest Island, one (*Conocyathus zelandiae*) to King George Sound, one (*Cyathelia axillaris*) to Esperance, and 3 (*Culicia australiensis*, *Conotrochus funiculumna*, and *Cyathotrochus pileus*) to the Great Australian Bight near Eucla. Thus the highest attrition rate of tropical species (50 species) appears to be the region between Cape Jaubert (coastal)–Rowley Shoals (oceanic) to Dampier Archipelago (coastal)–Glomar Shoal (oceanic).

Temperate West Australian Fauna.—Of the 26 azooxanthellate species that occur in the Southern Australian Warm Temperate Province (Table 1, column 5), 11 (11/26 = 42%) are endemic to this region. According to Morgan and Wells (1991), endemicity of shallow water benthic invertebrates and fish for this region is usually much higher (e.g., 63–95%); however, this discrepancy can be partially explained by the fact that whereas 10 of the 11 warm temperate endemics are shallow in distribution (Table 3), only 8 of the 15 non-endemic species occur in shallow water, the other 7 species being found deeper than 200 m and thus having the potential for a broader geographic range. Of these 11 endemic temperate species: 4 can be categorized as having a “Southeastern Australian” pattern (sensu Wilson and Allen 1987), being found only marginally off southeastern Western Australia in the Great Australian Bight; 5 extend to Albany/King George Sound region (“endemic south coast” pattern of Wilson and Allen 1987); and 2 species (i.e., *Trematotrochus verconis*, and *Rhizotrochus*

Table 3 General Bathymetric Ranges of Western Australian Azooxanthellate Species in relation to Distribution Pattern (see Table 1).

	0–200 m (shelf)	Intermediate (shelf+slope)	> 200 m (slope)
TROPICAL			
1A (Widespread)	3	0	3
1B (IWP)	14	1	8
1C (W. Pacific)	9	4	16
1D (Amphi-Indian)	1	0	1
1E (Endemic)	7	0	2
TROPICAL and TEMPERATE			
2A (Widespread)	5	1	13
2B (Endemic)	1	0	0
ENDEMIC TEMPERATE			
3A (southern Australia)	10	0	1
3B (s. Australia and S. Africa)	0	0	1
Unclassified	3	0	1
TOTAL:	53	6	46

tuberculatus) extend to the Houtman Abrolhos Islands ("Southwestern Australian" pattern of Wilson and Allen, 1987).

Four species were not categorized because of their unusually disjunct distributions: *Letepsammia fissilis*, *Cyathelia axillaris*, *Crispatotrochus inornatus*, and *Dendrophyllia boschmai*.

Check List of Western Australian Azooxanthellate Scleractinia

Order Scleractinia

Suborder Fungiina

Superfamily Fungioidea Dana, 1846

Family FUNGIACYATHIDAE, Chevalier 1987

Fungiacyathus (F.) *stephanus* (Alcock, 1893)

F. (F.) *fragilis* Sars, 1872

F. (F.) *paliferus* (Alcock, 1902)

F. (F.) *multicarinatus* sp. nov.

F. (*Bathyactis*) *variegatus* Cairns, 1989

F. (B.) *granulosus* Cairns, 1989

Family MICRABACIIDAE Vaughan, 1905

Letepsammia formosissima (Moseley, 1876)

L. *fissilis* Cairns, 1995

Rhombopsammia niphada Owens, 1986

Stephanophyllia complicata Moseley, 1876

Suborder Faviina

Family RHIZANGIIDAE d'Orbigny, 1851

Culicia australiensis Hoffmeister, 1933

C. *hoffmeisteri* Squires, 1966

Astrangia atrata (Dennant, 1906)

Oulangia stokesiana Milne Edwards and Haime, 1848

Family Oculinidae Gray, 1847 OCULINIDAE

Madrepora oculata Linnaeus, 1758

Cyathelia axillaris (Ellis and Solander, 1786)

Family ANTHEMIPHYLLIIDAE Vaughan, 1907

Anthemiphyllia dentata (Alcock, 1902)

Suborder Caryophylliina

Superfamily Caryophylloidea Dana, 1846

Family CARYOPHYLLIIDAE Dana, 1846

Caryophyllia (C.) *transversalis* Moseley, 1881

C. (C.) *rugosa* Moseley, 1881

C. (C.) *quadrigenaria* Alcock, 1902

C. (C.) *stellula* sp. nov.

C. (C.) *atlantica* (Duncan, 1873)

C. (C.) *grandis* Gardiner and Waugh, 1938

C. (*Acanthocyathus*) *grayi* (Milne Edwards and Haime, 1848)

C. (A.) *unicristata* Cairns and Zibrowius, 1997

C. (A.) *decamera* sp. nov.

Crispatotrochus rugosus Cairns, 1995

C. *inornatus* Tenison Woods, 1878

Oxysmilia circularis sp. nov.

Trochocyathus philippinensis Semper, 1872

T. *apertus* Cairns and Zibrowius, 1997

Paracyathus rotundatus Semper, 1848

P. ?*fulvus* Alcock, 1893

Stephanocyathus (*Acinocyathus*) *spiniger* (Marenzeller, 1888)

S. (A.) *explanans* (Marenzeller, 1904)

Deltocyathus magnificus Moseley, 1876

D. *suluensis* Alcock, 1902

D. *sarsi* (Gardiner and Waugh, 1938)

Heterocyathus aequicostatus Milne Edwards and Haime, 1848

H. *alternatus* Verrill, 1865

H. *sulcatus* (Verrill, 1866)

H. *hemisphaericus* Gray, 1849

Conotrochus funiculumna (Alcock, 1902)

Paraconotrochus zeidleri Cairns and Parker, 1992

Desmophyllum dianthus (Esper, 1794)

Thalamophyllia tenuescens (Gardiner, 1899)

Asterosmilia marchadi (Chevalier, 1966)

"*Rhizosmilia*" *multipalifera* sp. nov.

Solenosmilia variabilis Duncan, 1873

Family TURBINOLIIDAE Milne Edwards and Haime, 1848

Trematotrochus verconis Dennant, 1904

T. *alternans* Cairns and Parker, 1992

Conocyathus zelandiae Duncan, 1876

C. *gracilis* sp. nov.

Alatotrochus rubescens (Moseley, 1876)

Platyatrochus laevigatus Cairns and Parker, 1992

P. *hastatus* Dennant, 1902

Idiotrochus kikutii (Yabe and Eguchi, 1941)

Notocyathus venustus (Alcock, 1902)

Tropidocyathus lessonii (Michelin, 1842)

"T." *labidus* Cairns and Zibrowius, 1997

Cyathotrochus pileus (Alcock, 1902)

Australocyathus vincentinus (Dennant, 1904)

Deltocyathoides orientalis (Duncan, 1876)

Superfamily Flabelloidea Bourne, 1905

Family GUYNIIDAE Hickson, 1910

Guynia annulata Duncan, 1872

Family FLABELLIDAE Bourne, 1905

Flabellum (F.) *magnificum* Marenzeller, 1904

F. (F.) *lamellulosum* Alcock, 1902

F. (F.) *patens* Moseley, 1881

F. (F.) *folkesoni* sp. nov.

F. (F.) *politum* Cairns, 1989

F. (*Ulocyathus*) *hoffmeisteri* Cairns and Parker, 1992

F. (U.) *tuthilli* Hoffmeister, 1933

F. (U.) *marenzelleri* Cairns, 1989

F. (U.) *deludens* Marenzeller, 1904

Truncatoflabellum angiosomum (Folkeson, 1919)

T. *formosum* Cairns, 1989

T. *australiensis* sp. nov.

T. *paripavoninum* (Alcock, 1894)

T. *spheniscus* (Dana, 1846)

T. *aculeatum* (Milne Edwards and Haime, 1848)

T. *veroni* sp. nov.

T. *macroeschara* sp. nov.

Placotrochus laevis Milne Edwards and Haime, 1848

Javania lamprotichum (Moseley, 1880)

Rhizotrochus tuberculatus (Tenison Woods, 1878)

Polymyces wellsi Cairns, 1991

Gardineria hawaiiensis Vaughan, 1907

G. philippinensis Cairns, 1989

Suborder Dendrophylliina

Family DENDROPHYLLIIDAE Gray, 1847

Balanophyllia carinata (Semper, 1872)

B. imperialis Kent, 1871

B. gigas Moseley, 1881

B. cornu Moseley, 1881

B. generatrix Cairns and Zibrowius, 1997

Endopachys grayi Milne Edwards and Haime, 1848

E. bulbosa Cairns and Zibrowius, 1997

Notophyllia recta Dennant, 1906

N. piscacauda sp. nov.

Heteropsammia cochlea (Spengler, 1781)

Leptopsammia columna Folkesson, 1919

Rhizopsammia verrilli van der Horst, 1922

Dendrophyllia alcocki (Wells, 1954)

D. arbuscula van der Horst, 1922

D. boschmai van der Horst, 1926

Tubastraea coccinea Lesson, 1829

T. diaphana (Dana, 1846)

T. micranthus (Ehrenberg, 1834)

SYSTEMATICS

Order Scleractinia

Suborder Fungiina

Superfamily Fungioidea Dana, 1846

Family Fungiacyathidae Chevalier, 1987

Genus *Fungiacyathus* Sars, 1872

Subgenus *Fungiacyathus* Sars, 1872

Fungiacyathus (F.) *stephanus* (Alcock, 1893)

Bathyactis stephanus Alcock, 1893: 149, pl. 5, figs. 12, 12a.

Fungiacyathus (F.) *stephanus* – Cairns, 1989: 7–9, pl. 1, figs. a–k, pl. 2, figs. a–b (synonymy and description); 1995: 31–32, pl. 1, figs. a–c.—Cairns and Zibrowius, 1997: 68–69.

New Records

Soela: stn 02/82/19, 1 concave, WAM 300–88; stn 02/82/22, 1 concave, WAM 25–83; stn 02/82/26, 1 concave, WAM 32–83; stn 02/82/27, 1 concave, WAM 479–96; stn 02/82/31, 2 concave, USNM 97800; stn 02/82/34, 2 concave, WAM 30–83; stn 02/82/40, 1 flat, WAM 37–83; stn 01/84/64, 10 flat, WAM 767–84; stn 01/84/67, 11 flat: 8 (WAM 724–84), 3 (USNM 97801).

Courageous: stn 003, 2 concave, WAM 427–96; stn 020, 1 flat, WAM 66–84.

Remarks

Two forms of this species were described by Cairns and Zibrowius (1997), one having a flat base, the other a concave base (see New Records). Off Western Australia the flat-based form was found at a shallower depth (304–450 m) than the concave-based form (452–720 m).

Distribution

Western Australia: continental slope of northwestern coast from south of Scott Reef to Port Hedland; 304–720 m; 8.4°–10.7°C; always reported on a soft/mud substrate. Elsewhere: Indo-West Pacific (widespread from southwestern Indian Ocean to Kermadec Ridge, including Japan); 245–2000 m (Cairns and Zibrowius 1997).

Fungiacyathus (F.) *fragilis* Sars, 1872

Fungiacyathus fragilis Sars, 1872: 58, pl. 5, figs. 24–32.—Cairns, 1982: 7, pl. 1, figs. 3–7 (synonymy); 1995: 32, pl. 1, figs. d–f (synonymy); in press, Table 3.

New Records

Lady: stn RW96–29, 1, NTM C8088; stn RW96–31, 1, NTM C8091.

Remarks

Fungiacyathus fragilis is similar to the previous species but can be distinguished by lacking paliform lobes (P2) and having much lower septal lobes. It is compared to all other species in the subgenus by Cairns (in press, Table 3). The specimen from *Lady* stn RW96–31 is 52 mm in calicular diameter, the largest known corallum of this species.

Distribution

Western Australia: continental slope of northwestern coast between Browse and Cartier Islands; 400–420 m. Elsewhere: cold temperate New Zealand; cold temperate North Atlantic; Hawaiian Islands; 285–2200 m (Cairns 1995).

Fungiacyathus (F.) *paliferus* (Alcock, 1902a)

Bathyactis palifera Alcock, 1902a: 108; 1902c: 38, pl. 5, figs. 34, 34a.—Hoffmeister, 1933: 14, pl. 4, fig. 6.

Fungiacyathus (F.) *paliferus* – Cairns, 1989: 9–10, pl. 2, figs. c–i, pl. 3, figs. a–c (synonymy and description).—Cairns and Parker, 1992: 6–7, pl. 1, figs. a–b.—Cairns and Zibrowius, 1997: 69–70.

New Records

Soela: stn 1/79/unnumbered, 2 irregular fragments, WAM 33–85; stn 1/79/18, 1, USNM

97802; stn 02/82/13A, 1 irregular fragment, WAM 478–96.

Umataka Maru: stn 6291, 2 irregular fragments, WAM 428–96.

Lady: stn RW96–17, 1, NTM C8071.

Remarks

This species is also known to occur in two growth forms: relatively large (GCD over 2 cm), complete coralla, and as irregularly-shaped (often semi-circular) regenerative fragments less than 1 cm in GCD (Cairns 1994). Three of the lots reported are irregular fragments, one of the other two (i.e., *Soela* 1/79/18) being one of the largest known specimens, having a GCD of 25.1 mm.

Distribution

Western Australia: continental shelf of northwestern coast from Cartier Island to west of Glomar Shoal; 101–300 m. Elsewhere: Indo-West Pacific (southwestern Indian Ocean to Japan, including Great Australian Bight (western South Australia)); 69–823 m (Cairns and Zibrowius 1997).

Fungiacyathus (F.) multicarinatus sp. nov.

Figure 1 a–c

Records

Soela: stn 01/84/54, holotype, WAM 547–84.

Description

Corallum circular, but eccentric, caused by regeneration from a parent fragment that composes about one-third of corallum; GCD = 25.9 mm. Base undulating, also due to regeneration. Costae finely dentate, low ridges. Septa hexamerally arranged in five cycles; all septa planar, with straight upper edges. S1 bear 30–34 trabecular carinae on each face, sometimes aligned on either side of a septum, but usually not. Septal carinae quite tall, up to 0.4 mm, filling most of interseptal regions and obscuring view of corallum base and synapticalae. Innermost trabecular carinae produced into spatulate spines that arch toward and slightly over the columella. Middle and outer trabecular carinae grouped into upward projecting spines of 2 or 4 trabeculae apiece. S2 similar to S1 but slightly smaller. S3 similar to S2 but slightly less tall and composed of only 24–26 trabecular per septal face. Inner edges of S1–3 extend to columella. S4 bear only 16–18 trabecular carinae per face, fusing to their adjacent S3 about two-thirds distance to columella. S5 rudimentary, composed of only 5–7 trabecular carinae per septal face, merging with their common S4 about half distance to columella. No septal canopies; no pali or paliform lobes. Synapticalae small and poorly developed. Columella papillose.

Remarks

This subgenus consists of five Recent species: *F. pusillus* (Pourtales, 1868); *F. fragilis* Sars, 1872; *F. stephanus* (Alcock, 1893); *F. paliferus* (Alcock, 1902a); and *F. sp.* A sensu Cairns, 1994. *F. multicarinatus* differs from these species in having more numerous and much taller trabecular carinae, and poorly developed synapticalae. Although represented by only one specimen, it would appear to be a species that reproduces by asexual fragmentation, a mode consistent with its poorly developed synapticalae.

Distribution

Western Australia: continental slope off Dampier Land; 348–350 m.

Etymology

The species name *multicarinatus* (Latin *multus*, many + *carinatus*, keeled, carinate) alludes to the numerous trabecular carinae on the face of each septum, more than in any other species in the genus.

Subgenus *Bathyactis* Moseley, 1881

Fungiacyathus (B.) variegatus Cairns, 1989

Fungiacyathus (B.) variegatus Cairns, 1989: 11–12, pl. 5, figs. a–h; 1994: 38–39, pl. 15, figs. a–b.—Cairns and Zibrowius, 1997: 71–72.

New Records

Soela: stn 01/84/65, 2, WAM 1020–85.

Umataka Maru: stn 6921, 1, WAM 148–84.

Distribution

Western Australia: continental slope of northwestern coast south of Scott Reef and south of Rowley Shoals; 300–302 m. Elsewhere: western Pacific from Ryukyu Islands through Indonesia; 84–715 m (Zibrowius and Cairns, 1997).

Fungiacyathus (B.) granulosus Cairns, 1989

Fungiacyathus (B.) granulosus Cairns, 1989: 11, pl. 4, figs. d–i; 1994: 39, pl. 15, figs. d–e.—Cairns and Zibrowius 1997: 71.

New Records

Soela: stn 01/84/65, 8: 5 (WAM 768–84), 3 (USNM 97803); stn 01/84/66, 3, WAM 741–84; stn 01/84/67, 5, WAM 429–96; stn 01/84/77, 1, WAM 526–84; stn 01/84/122, 1, WAM 794–84.

Courageous: stn 002, 2, WAM 452–96; stn 004, 1, USNM 97804.

Distribution

Western Australia: continental slope of

northwestern coast off Seringapatam Reef to south of Rowley Shoals; 302–400 m on exclusively soft, muddy substrates. Elsewhere: western Pacific from Ryukyu Islands through Indonesia; 287–640 m (Cairns and Zibrowius 1997).

Family Micrabaciidae Vaughan, 1905

Genus *Letepsammia* Yabe and Eguchi, 1932

Letepsammia formosissima (Moseley, 1876)

Stephanophyllia formosissima Moseley, 1876: 561–562.

Letepsammia formosissima – Cairns, 1989: 15–18, pl. 6, fig. j, pl. 7, figs. g–i, pl. 8, figs. a–d (synonymy and description).—Cairns and Parker, 1992: 8–9, pl. 1, figs. f, h.—Cairns and Keller, 1993: 230–231, pl. 3, fig. D.—Cairns, 1995: 36–37, pl. 3, figs. f–g.—Cairns and Zibrowius, 1997: 73–75.

New Records

Soela: stn 01/84/51, 2, WAM 542–84; stn 01/84/56, 1, WAM 566–84; stn 01/84/116, 4: 2 (WAM 697–84), 2 (USNM 97805); stn 01/84/118, 1, WAM 779–84; stn 01/84/121, 2, WAM 789–84.

Umatoka Maru: stn 6922, 1, WAM 1022–85.

Distribution

Western Australia: continental slope of northwestern coast from Dampier Land to southwest of Rowley Shoals; 302–500 m on soft, muddy substrates. Elsewhere: widespread, from southwestern Indian Ocean to Hawaiian Islands, including South China Sea, Philippines, Indonesia, Norfolk and Kermadec Ridges, and southeastern Australia; 97–457 m (Cairns and Parker 1992; Cairns 1995; Cairns and Zibrowius 1997).

Letepsammia fissilis Cairns, 1995

Letepsammia fissilis Cairns, 1995: 35–36, pl. 3, figs. a–e.

New Record

Soela: stn 02/82/13A, 1, WAM 89–84.

Distribution

Western Australia: southwest of Rowley Shoals; 201 m. Elsewhere: New Zealand region (northern North Island and Norfolk Ridge); 106–206 m.

Genus *Rhombopsammia* Owens, 1986

Rhombopsammia niphada Owens, 1986

Rhombopsammia niphada Owens, 1986: 252–255, figs. 2b, 3a–d.—Cairns, 1989: 19–20, pl. 9, figs. d–j, text-fig. 2 (synonymy and description); 1994: 41,

pl. 15, figs. i–k, pl. 16, fig. e.—Cairns and Zibrowius, 1997: 75–76.

New Records

Soela: stn 02/82/19, 1, WAM 22–83; stn 02/82/27, 1, WAM 34–83; stn 01/84/51, 2, WAM 430–96; stn 01/84/77, 6: 3 (WAM 522–84), 3 (USNM 97806); stn 01/84/81, 1, WAM 672–84; stn 01/84/120, 1, WAM 431–96; stn 01/84/121, 1, WAM 790–84.

Distribution

Western Australia: continental slope of northwestern coast from Cartier Island to Port Hedland; 390–696 m on soft, muddy substrates. Elsewhere: western Pacific from Japan through Indonesia; 405–804 m (Cairns and Zibrowius 1997).

Genus *Stephanophyllia* Michelin, 1841

Stephanophyllia complicata Moseley, 1876

Stephanophyllia complicata Moseley, 1876: 558–561, text-fig.—Cairns, 1989: 21, pl. 12, figs. a–b; 1995: 37–38, pl. 3, fig. h, pl. 4, figs. a–e (synonymy and description).—Cairns and Zibrowius, 1997: 77–78.

New Records

Soela: stn 01/84/99, 2, USNM 97807; stn 01/84/100, 1, WAM 690–84; stn 01/84/102, 1, WAM 771–84; stn 01/84/105, 3, WAM 786–84; stn 01/84/109, 2, WAM 692–84; stn 01/84/112, 1, USNM 97808.

Umatoka Maru: stn 6920, 3, WAM 131–84; stn 6921, 4, WAM 152–84; stn 6922, 1, WAM 1023–85; stn 6926, 1, WAM 100–84; stn 6930, 1, WAM 252–93.

Diamantina: stn 186, 1, WAM 155–83.

Remarks

The largest corallum known of this species is from Western Australia (*Soela* stn 01/84/112), measuring 23.8 mm in calicular diameter.

Distribution

Western Australia: continental slope of northwestern coast from near Browse Island to Cape Farquhar, but most records reported above from Rowley Shoals; 260–433 m on soft substrates. Elsewhere: western Indian Ocean; Banda Sea; Norfolk and Three Kings Ridge; 210–1137 m (Cairns and Zibrowius 1997).

Suborder Faviina

Family Rhizangiidae d'Orbigny, 1851

Genus *Culicia* Dana, 1848

Culicia australiensis Hoffmeister, 1933

Culicia australiensis Hoffmeister, 1933: 12, pl. 3, figs. 3–4.—Cairns and Parker, 1992: 12–13, pl. 2, figs. a, d, g (synonymy and description).

Culicia sp. Veron, 1986: 600, black and white fig.

New Records

Soela: stn 05/82/55, 2, WAM 72–83.

Franklin: stn GAB033, 3, SAM H874.

Kunmuntah: stn BG141, 2, NTM C8032.

Comet: 33°17'S, 128°12'E, 180 m, 13 I 1989, 2, SAM H868.

Other records: Flying Fish Cove, Christmas Island, 0–3 m, 22 II 1987, 1, WAM 614–87; 13°56'S, 125°37'E (Cassini Island, Kimberley), "SCUBA" depth, 18 VIII 1991, 1, WAM 147–91 (attached to base of *Rhizopsammia verrilli*); North Mole, Fremantle Harbour, 25 XI 1983, 1, USNM 97809; Geographe Bay, Dunsborough, 18 m, 26 I 1978, 4, WAM 311–78;

Distribution

Western Australia: entire coastline; 18–180 m. Elsewhere: South Australia (Cairns and Parker 1992); Peron Islands, Northern Territory (reported herein); Christmas Island; 3–238 m.

Culicia hoffmeisteri Squires, 1966

Culicia hoffmeisteri Squires, 1966: 171–172, pl. 1, fig.

3.—Cairns and Parker, 1992: 13–14, pl. 3, figs. a–d (synonymy and description).

New Record

Frenchman Bay, Albany, Western Australia (35°05'S, 117°57'E), 0–10 m, 17 XII 1982, 1 colony, NMV F78388.

Distribution

Western Australia: continental shelf off Albany; 0–10 m. Elsewhere: South Australia; 0–29 m (Cairns and Parker 1992).

Genus *Astrangia* Milne Edwards and Haime, 1848d

Astrangia atrata (Dennant, 1906)

Dendrophyllia atrata Dennant, 1906: 163–165, pl. 6, figs. 5a–b.

Astrangia atrata – Cairns and Parker, 1992: 14, figs. 3e–g (synonymy and description).

New Record

Franklin: stn GAB 063, 1 colony, SAM H869.

Distribution

Western Australia: known only from Great Australian Bight off Point Culver; 46 m. Elsewhere: southeastern Australia (New South Wales to South Australia); 9–40 m (Cairns and Parker 1992).

Genus *Oulangia* Milne Edwards and Haime, 1848c

Oulangia stokesiana stokesiana Milne Edwards and Haime, 1848c

Figure 1 d–e

Oulangia stokesiana Milne Edwards and Haime, 1848c: pl. 7, figs. 4, 4a; 1849:183; 1850b: xiv.—Faustino, 1927: 111 (translation of original description).

?*Qulangia* (*sic*) *stokesiana* – Zou, 1988: 78, pl. 4, figs. 1–3.

New Records

Kunmuntah: stn BG69, 3, NTM C8018.

Other records: Black Rocks area, north of Derby, King Sound, intertidal, X 1975, 1, WAM 153–83

Remarks

This rarely reported species is known only from the holotype, which is probably lost (Milne Edwards and Haime 1860: 108), and specimens reported by Zou (1988), which are doubtful in identification. The Western Australian specimen figured below agrees well with the original description except for being slightly smaller (9.6 × 7.1 mm in calicular diameter, 6.8 mm in height, and 6.1 mm in pedicel diameter) and in having a uniform black-brown pigmentation on the calicular elements that extends to the theca within 1 mm from the calicular edge. It contains 96 septa: one half system lacks a pair of S5 and another has a pair of S6.

The other subspecies, *Oulangia stokesiana miltoni*, described by Yabe and Eguchi (1932), is known from Japan and South Korea (Cairns, 1994).

Distribution

Western Australia: King Sound, Kimberley; intertidal reef rock. Elsewhere: Fog Bay, Northern Territory (reported herein); Philippines; ?South China Sea (Zou 1988); 1–6 m.

Family Oculinidae Gray, 1847

Genus *Madrepora* Linnaeus, 1758

Madrepora oculata Linnaeus, 1758

Figure 1 f–i

Madrepora oculata Linnaeus, 1758: 798.—Cairns, 1994: 18–19, pl. 3, figs. f–h (synonymy and description).—Grygier and Cairns, 1997: 63–64, 68, figs. 1A–F.—Cairns and Zibrowius, 1997: 79–80.

Madrepora sp. Veron, 1986: 599, black and white fig.

New Records

Soela: stn 01/84/49, 1, WAM 765–84; stn 01/84/

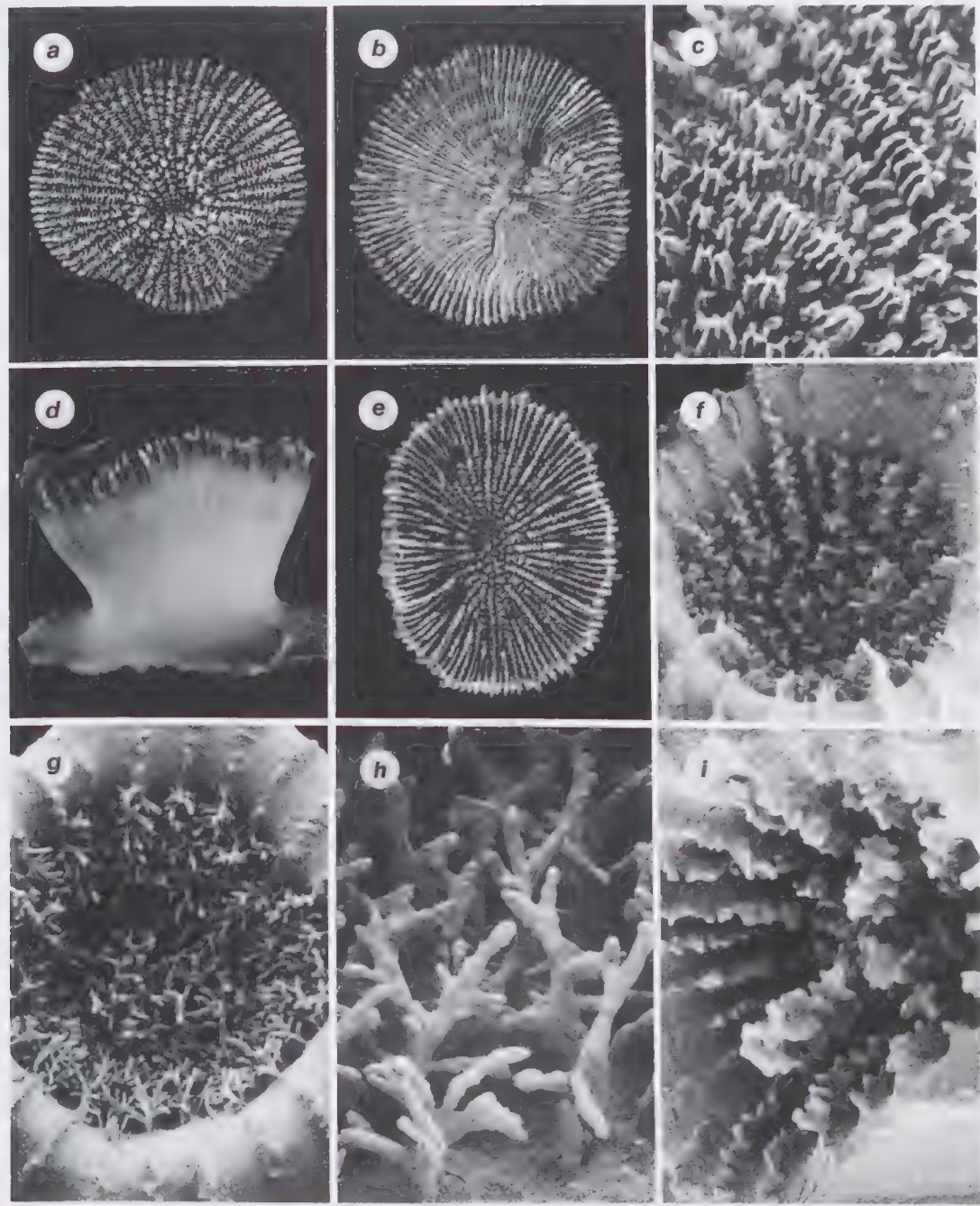


Figure 1 a-c, *Fungiacyathus multicarinatus*, holotype: a-b, calicular and basal views, x 1.68; c, detail of highly ridged septal faces, x 7.9. d-e, *Oulangia stokesiana*, Derby, King Sound, WAM 152-83, side and calicular views, x 5.1. f-i, *Madrepora oculata*: f, typical corallite, Soela stn 01/84/52, USNM 97811, x 34; g-h, corallite with highly modified, spinose septa, Soela stn 01/84/107, WAM 733-84, x 30, x 140, respectively; i, corallite with asymmetrically developed P2, Soela stn 01/84/99, WAM 755-84, x 42.

51, *2, WAM 801–84; stn 01/84/52, *3: 2 (WAM 544–84), 1, including SEM stub 853 (USNM 97811); stn 01/84/54, 5, WAM 551–84; stn 01/84/64, 1, WAM 583–84; stn 01/84/67, 1, WAM 669–84; stn 01/84/70, 5, WAM 530–84; stn 01/84/72, 1, WAM 795–84; stn 01/84/75, *1, WAM 787–84; stn 01/84/76, 1, WAM 799–84; stn 01/84/78, *6, USNM 97812; stn 01/84/80, *1, WAM 722–84; stn 01/84/81, *1, WAM 763–84; stn 01/84/82, 1, WAM 760–84; stn 01/84/82a, 1, WAM 750–84; stn 01/84/91, 1, WAM 751–84; stn 01/84/94, 2, WAM 725–84; stn 01/84/96, 2, WAM 753–84, and SEM stub 850 (USNM); stn 01/84/98, 1, WAM 772–84; stn 01/84/99, *3, WAM 755–84, and SEM stub 852 (USNM); stn 01/84/101, 1, WAM 726–84; stn 01/84/102, *1, WAM 770–84; stn 01/84/105, *3, WAM 734–84; stn 01/84/107, 1, WAM 733–84, and SEM stub 851 (USNM); stn 01/84/108, *3, USNM 97813; stn 01/84/109, *3, WAM 7–87, and SEM stub 849 (USNM); stn 01/84/111, 1, WAM 774–84; stn 01/84/112, *2, WAM 776–84; stn 01/84/113, 1, WAM 777–84; stn 01/84/118, *1, WAM 781–84.

Courageous: stn 004, 2, WAM 74–84; stn 013, 1, WAM 73–84; stn 015, 8: 4 (WAM 105–840), 4 (USNM 97810).

Remarks

Grygier and Cairns (1997) illustrated several extremely enlarged, highly modified corallites of Western Australian *M. oculata* that were caused by the infestation of petraroid ascothoracid crustaceans. The 12 Western Australian records cited by Grygier and Cairns (1997) are reiterated above, and constitute an infestation rate of 39.4% (13/33 lots listed above marked with an asterisk) of the lots known from Western Australia. However, even corallites not affected by parasites show great variation in calicular features. Some coralla have a deep fossa and no pali or columella, whereas others have a shallow fossa and well-developed P2 and columella (Figure 1f). Several coralla were noted to have asymmetrically developed P2, bearing 2 or 3 enlarged P2, the other P2 being rudimentary (Figure 1i). Still another corallum possessed several corallites in which the septal and columellar elements had been reduced to a thicket of elongate spines (Figure 1g–h). Those coralla in which the P2 and columella are well developed resemble the genus *Sclerhelia* Milne Edwards and Haime, 1850a; however, the P2 and columella are much more robust in that genus. Nonetheless, a revision of the Oculinidae may lead to the synonymy of *Sclerhelia* with *Madrepora* or, conversely, the splitting of the *Madrepora oculata* into several species.

Distribution

Western Australia: continental slope of northwestern coast from Cartier Island to

southwest of Rowley Shoals; 304–544 m, usually on a soft (mud) substrate. Elsewhere: virtually cosmopolitan, except for continental Antarctica and southern Australia; 15–1500 m (Cairns and Zibrowius 1997).

Genus *Cyathelia* Milne Edwards and Haime, 1849

Cyathelia axillaris (Ellis and Solander, 1786)

Madrepora axillaris Ellis and Solander, 1786: 153, pl. 13, fig. 5.

Cyathelia axillaris – Veron, 1986: 599, color and black and white figs.—Cairns, 1994: 43–44, pl. 18, figs. a–c (synonymy and description).—Cairns and Zibrowius, 1997: 84.

New Record

East side Thomas Island, Esperance, 9–12 m (back of cave), 6 III 1977, 1 large colony, WAM 623–79.

Remarks

This colony differs from those previously reported in having a completely white corallum, the others having a tan corallum with dark brown corallites. When alive, however, this colony was reported to have brown polyps. The Esperance specimen is the largest known corallum, measuring 15 cm tall and having a massive base 5.5 cm in diameter.

Distribution

Western Australia: Recherche Archipelago (Veron 1986) and Esperance; 12–40 m. Elsewhere: western Pacific from Japan through Indonesia; 13–366 m (Cairns and Zibrowius 1997).

Family Anthemiphylliidae Vaughan, 1907

Genus *Anthemiphyllia* Pourtalès, 1878

Anthemiphyllia dentata (Alcock, 1902a)

Discotrochus dentatus Alcock, 1902a: 104.

Anthemiphyllia dentata – Veron, 1986: 604, fig.—Cairns and Parker, 1992: 16–17, pl. 4, figs. e–f.—Cairns, 1995: 41–42, pl. 6, figs. c–g (synonymy and description).—Cairns and Zibrowius, 1997: 86.

New Records

Soela: stn 02/82/10A, 1, WAM 45–84; stn 02/82/13A, 2, WAM 78– and 91–84.

Lady: stn RW96–17, 1 NTM C8073.

Lady Basten: stn LB5(s), 2, WAM 32–96.

Distribution

Western Australia: Great Australian Bight, off

Eucla (Cairns and Parker 1992); off Port Hedland; south of Cartier Island; 154–240 m. Elsewhere: Indo-West Pacific (widespread from southwestern Indian Ocean to Japan, including Kermadecs and southeastern Australia); 50–570 m (Cairns and Zibrowius 1997).

Suborder Caryophylliina

Family Caryophylliidae Dana, 1846

Genus *Caryophyllia* Lamarck, 1801

Subgenus *Caryophyllia* Lamarck, 1801

Caryophyllia (C.) *transversalis* Moseley, 1881

Caryophyllia clavus var. *transversalis* Moseley, 1881: 134–135, pl. 1, figs. 2, 2a.

Caryophyllia (C.) *transversalis* – Cairns and Zibrowius 1997: 90–91, figs 6 f–h (description).

New Records

Soela: stn 01/84/74, 1, WAM 533–84; stn 01/84/78, 1, USNM 97814; stn 01/84/85, 2, WAM 683–84; stn 01/84/87, 1, WAM 685–84.

Umataka Maru: stn 6921, 3, WAM 154–84; stn 6930, 1, WAM 241–93.

Distribution

Western Australia: continental slope of northwestern coast from Browse Island to south of Rowley Shoals; 224–302 m. Elsewhere: Indonesia; 210–397 m (Cairns and Zibrowius 1997).

Caryophyllia (C.) *rugosa* Moseley, 1881

Caryophyllia rugosa Moseley, 1881: 141–143, pl. 1, figs. 8a–b.—Cairns, 1994: 47, pl. 20, fig. i, pl. 21, fig. a (synonymy and description); 1995: 43–44, pl. 6, fig. h, pl. 7, figs. a–c.—Cairns and Zibrowius, 1997: 91–92.

New Records

Soela: stn 05/82/36, 2: 1 (WAM 67–83), 1 (USNM 97815).

Lady Basten: stn LB7(s), 1, WAM 456–96.

Distribution

Western Australia: south of Rowley Shoals and off Port Hedland; 180–200 m; 17.4°C. Elsewhere: widespread in Indo-Pacific from southwestern Indian Ocean to Hawaiian Islands, including Japan and Kermadec Islands; 71–508 m (Cairns and Zibrowius 1997).

Caryophyllia (C.) *quadrigenaria* Alcock, 1902a

Caryophyllia quadrigenaria Alcock, 1902a: 91–92.—Cairns, 1995: 45–46, pl. 7, figs. g–h

(synonymy and description).—Cairns and Zibrowius, 1997: 93.

New Records

Soela: stn 02/82/10A, 4: 2 (WAM 44–84), 2 (USNM 97816); stn 02/82/13A, 1, WAM 84–84.

Distribution

Western Australia: off Port Hedland; 154–201 m on rubble substrate. Elsewhere: western Pacific from Japan to New Zealand (Cairns and Zibrowius 1997); 54–385 m.

Caryophyllia (C.) *stellula* sp. nov.

Figure 2 a–c

Caryophyllia epithecata – Gardiner, 1904: 114–117 (in part: localities I–V; pl. 1, figs. 3 a–c).—Cairns and Keller, 1993: 219 [Not *Caryophyllia clavus* var. *epithecata* Duncan, 1873: 312–313, pl. 48, figs. 13–16 (=C. *smithii*)].

Records

Diamantina: stn 25, holotype and 11 paratypes: 7 (WAM 301–88), 4 (USNM 97817); stn 20, 1 paratype, WAM 250–93;

Comet: 33°19'S, 128°00–05'E, 240–245 m, 13–14 I 1989, 4 paratypes, SAM H853, 856, and 871; 33°20'S, 127°45–50'E, 240–260 m, 16 I 1989, 10 paratypes, SAM H852, 855, 857, 859; 33°19'S, 127°31'E, 240 m, 12 I 1989, 1 paratype, SAM H851.

Type Locality

31°48'S, 114°08'E (west of Rottneest Island); 402 m.

Description

Corallum ceratoid, often curved up to 90°, usually having a slender (0.6–1.3 mm diameter) eroded, unattached base. However, several coralla have a narrow attached pedicel, the PD:GCD only 0.11–0.15, these coralla also slightly curved. The base of one corallum encrusts a small shell fragment, and is in the process of enveloping it and becoming free of attachment. Calice elliptical: GCD:LCD = 1.08–1.37. Longest specimen (holotype) 11.7 × 10.7 mm in calicular diameter and 31.1 mm in length, having an open eroded base. Theca thick and sparsely covered with encrusting calcareous epifauna and often bored with tiny holes. Intercostal striae shallow, resulting in poorly defined costae; costal granulation low and inconspicuous, about 4 low, rounded granules occurring across the width of a costa. Theca thick, producing a dense corallum; theca adjacent to calicular edge light yellow-brown.

Septa hexamerally arranged in 4 cycles (S1–2>S3>S4), a full fourth cycle attained at a GCD as small as 6 mm. Specimen with largest calice

(SAM H851) 15.6 x 11.4 mm in diameter, having 2 pairs of S4 in one half-system, resulting in 52 septa and 13 pali (i.e., 11 P3 and 2 P4). S1–2 little exsert (0.8–1.4 mm), extend about 2/3 distance to columella, having slightly sinuous inner edges. S3 and S4 less exsert (0.6–0.8 mm), the S3 about 2/3 width of the S1–2, having highly sinuous inner edges. S4 about 4/5 width of the S3, having slightly sinuous inner edges. A well-defined crown on 12 P3, each palus 1.7–2.0 mm wide, occurs about 2 mm below calicular edge. Pali thin and coarsely granular, having sinuous edges. Fascicular columella composed of 3–10 slender, twisted elements, recessed 2 mm below upper edges of pali.

Remarks

Among the approximately 65 species of Recent *Caryophyllia* (see Cairns 1991; Best et al. 1995), *C. stellula* is unique in its tendency to pass through a stage having a narrow pedicel to an adult stage characterized by an unattached, cornute corallum. It is most similar to *C. squiresi* Cairns, 1992, known only from the Subantarctic region off Tierra del Fuego and the Falkland Islands at 646–845 m, but differs in having a smaller, more slender, and more curved corallum.

Gardiner (1904) reported specimens of *C. stellula* as "*Caryophyllia epithecata* n. sp." from South Africa, elevating Duncan's (1873) *Caryophyllia clavus* var. *epithecata* to the species level but treating it as a new species. However, according to the International Code of Zoological Nomenclature (1985: article 45g), a variety named before 1961 should be treated as a subspecies (or of the species rank), and therefore the correct author of *Caryophyllia epithecata* should be Duncan (1873). Regardless, Zibrowius (1974b) showed Duncan's variety *epithecata* to be a junior synonym of *C. smithii* and not conspecific with the South African species. Thus, this taxon, which is found off South Africa and now Western Australia, requires a new name. Zibrowius (1974b) also suggested that a specimen he reported as *Caryophyllia* sp. from St. Paul Island and *C. sewelli* Gardiner and Waugh, 1938 from the Red Sea were conspecific with Gardiner's (1904) specimens. This equivalence is doubted based on their thicker pedicels, straight coralla, and coarser pali.

Distribution

Western Australia: west of Rottnest Island; Great Australian Bight southwest of Eucla; 240–402 m. Elsewhere: southeastern (warm temperate) South Africa; 166–420 m (Gardiner 1904).

Etymology

The species name comes from the Latin *stellula*, meaning little star.

Caryophyllia (C.) *atlantica* (Duncan, 1873)

Bathycyathus atlanticus Duncan, 1873: 318, pl. 48, figs. 1–2.

Caryophyllia alcocki Vaughan, 1907: 73–74, pl. 5, fig. 1.

Caryophyllia atlantica – Zibrowius, 1980: 56–57, pl. 20, figs. A–K (synonymy and description).—Cairns, 1995: 47–48, pl. 8, figs. d–e (synonymy and description).

Caryophyllia pacifica Keller, 1981: 16–17, pl. 1, figs. 2a–b.

New Records

Soela: stn 01/84/49, 1, WAM 766–84; stn 01/84/54, 4, WAM 265–93; stn 01/84/55, 7: 4 (WAM 553–84), 3 (USNM 97819); stn 01/84/56, 2, WAM 565–84; stn 01/84/57, 1, WAM 735–84; stn 01/84/120, 1, WAM 1021–85; stn 01/84/122, 1, USNM 97818.

Umatata Maru: stn 6921, 1, WAM 433–96.

Lady Basten: stn LB6(s), 1, WAM 41–96.

Lady: stn RW96–18, 1, NTM C8094.

Remarks

The number of septa known for this species ranges from 48 (12 pali) to 72 (18 pali). All Western Australian specimens have the lower number of 48 septa and 12 pali, consistent with previously reported specimens from the central Pacific (Keller 1981).

Distribution

Western Australia: continental slope of northwestern coast south of Cartier Island to south of Rowley Shoals; 193–530 m, on soft and rubble substrates. Elsewhere: despite its provincial name this species is widely distributed, including the eastern Atlantic, central Pacific, and Campbell Rise; 776–2165 m.

Caryophyllia (C.) *grandis* Gardiner and Waugh, 1938

Caryophyllia grandis Gardiner and Waugh, 1938: 177, pl. 1, fig. 2.—Cairns and Keller, 1993: 234 (synonymy).—Cairns and Zibrowius, 1997: 96, figs. 7 g–h (diagnosis).

Caryophyllia sp. ?Veron, 1986: 605, black and white fig.

New Records

Soela: stn 02/82/35, 1, WAM 109–83; stn 01/84/77, 2, WAM 527–84; stn 01/84/79, 1, WAM 748–84; stn 01/84/81, 2, WAM 674–84; stn 01/84/82, 1, WAM 677–84; stn 01/84/92, 4, WAM 689–84; stn 01/84/100, 4, WAM 691–84; stn 01/84/111, 1, WAM 694–84; stn 01/84/120, 7: 4 (WAM 703– and

804–84), 3 (USNM 97820); stn 01/84/121, 1, WAM 793–84; stn 01/84/122, 1, WAM 731–84.

Courageous: stn 002, 1, WAM 56–84; stn 003, 6: 3 (WAM 57– and 72–84), 3 (USNM 96988); stn 011, 1, WAM 58–84; stn 013, 2, WAM 59–84; stn 015, 5, WAM 60–84; stn 033, 1, WAM 70–84.

Distribution

Western Australia: continental slope of northwestern coast from Cartier Island to off Port Hedland; 394–596 m. Elsewhere: tropical Indian Ocean; Indonesia; 183–595 m (Cairns and Zibrowius 1997).

Subgenus *Acanthocyathus* Milne Edwards and Haime, 1848a

Caryophyllia (A.) *grayi* (Milne Edwards and Haime, 1848a)

Acanthocyathus grayi Milne Edwards and Haime, 1848a: 293, pl. 9, figs. 2, 2a.

Caryophyllia (A.) *grayi* – Cairns, 1994: 49, pl. 21, figs. i–k (synonymy and description).—Cairns and Zibrowius, 1997: 97–98, figs. 7 c, f, i.

New Records

Soela: stn 05/82/47, 1, WAM 30–85.

Diamantina: stn 92, 1, WAM 138–83.

Lady Basten: stn LB5(s), 4, WAM 31–96; stn LB5(t), 1, WAM 15–96.

Remarks

The specimen from *Lady Basten* stn LB5(t), measuring 23.8 × 16.7 mm in calicular diameter and 32.5 mm in height, is the largest known corallum.

Distribution

Western Australia: continental shelf of western shelf off Cape Jaubert and Shark Bay (False Entrance); 130–150 m. Elsewhere: Indo-West Pacific from southwestern Indian Ocean to Japan; 37–490 m (Cairns and Zibrowius 1997).

Caryophyllia (A.) *unicristata* Cairns and Zibrowius, 1997

Caryophyllia (A.) *unicristata* Cairns and Zibrowius, 1997: 101–102, figs 9 d–e.

New Records

Soela: stn 01/84/52, 1, WAM 602–87; stn 01/84/65, 4: 2 (WAM 663–84), 2 (USNM 96989).

Courageous: stn 002, 1, WAM 61–84; stn 003, 2, WAM 68–84.

Distribution

Western Australia: continental slope of

northwestern coast from south of Scott Reef to southwest of Rowley Shoals; 302–450 m, on soft (muddy) substrates. Elsewhere: Arafura Sea; 251–477 m (Cairns and Zibrowius 1997).

Caryophyllia (A.) *decamera* sp. nov.

Figure 2 d–f

Caryophyllia (A.) *dentata* – Cairns and Zibrowius, 1997: 98 (in part: seven lots of decamerall specimens, fig. 8 b, d).

Records

DEKI: stn 3, holotype (USNM 96858) and 4 paratypes (USNM 96849).

KARUBAR: stn 49, 1 paratype, USNM 96956; stn 65, 3 paratypes, USNM 96857.

Soela: stn 01/84/85, 1 paratype, WAM 681–84.

Umataka Maru: stn 6920, 6 paratypes, WAM 132– and 134–84.

Type Locality

5°32'S, 132°36'E (Banda Sea, Kei Islands), 245 m.

Description

Corallum compressed (GCD:LCD = 1.3–1.4) and usually curved 90° in plane of GCD. Holotype 12.5 × 9.3 mm in calicular diameter and 13.4 mm in height. Pedicel small (1.2–1.5 mm in diameter) and circular in cross section. C1–2 low and rounded, covered with low, rounded granules. C1 on convex thecal edge ridged, bearing 4 or 5 prominent spines; one spine also often present on concave thecal edge. Corallum light brown. Septa decamerally arranged in 3 size classes (10:10:20, 40 septa). Primary septa highly exsert (up to 2.8 mm), each pair forming a rectangular lancet with its adjacent tertiaries. Inner edges of primary septa moderately sinuous. Secondary septa half width of primaries, having very sinuous inner edges. Tertiary septa 1/3 to 1/2 width of a secondary, having moderately sinuous inner edges. A crown of 10 lamellar, highly sinuous pali occurs before the secondary septa. Fossa of moderate depth, containing a fascicular columella composed of 3–8 slender twisted elements.

Remarks

As noted by Cairns and Zibrowius (1997), several specimens they identified as *C. dentata* were atypical in having decamerall symmetry. Those specimens, combined with additional coralla from Western Australia, form the basis of the description of *C. decamera*. To reiterate and amplify, *C. decamera* differs from *C. dentata* in having: decamerall septal symmetry, instead of hexamerall symmetry (i.e., 40 septa vs 48 septa); low, granular costae, not highly ridged costae; a tendency to have a single costal spine on the concave thecal edge;

and a tendency to have a curved corallum, instead of being straight.

Distribution

Western Australia: continental slope of northwestern coast from Kimberley to Rowley Shoals; 224–260 m. Elsewhere: Indonesia (Banda Sea, Arafura Sea); 176–263 m (Cairns and Zibrowius 1997).

Etymology

The species name *decamera* (Latin *decem*, ten + *camera*, chamber) alludes to the decamerall symmetry of the species resulting in ten equal chambers, or systems, of septa.

Genus *Crispatotrochus* Tenison Woods, 1878b

Crispatotrochus rugosus Cairns, 1995

Crispatotrochus rugosus Cairns, 1995: 57, pl. 13, figs. a–b.—Cairns and Zibrowius, 1997: 104.

New Record

Soela: stn 01/84/55, 6, WAM 560–84 and 453–96.

Distribution

Western Australia: continental slope off Cape Leveque, Dampier Land; 296–298 m. Elsewhere: Philippines; Malaysia; Kermadec Islands; Lord Howe Seamount Chain; 142–508 m (Cairns and Zibrowius 1997).

Crispatotrochus inornatus Tenison Woods, 1878b

Figure 2 g–h

Crispatotrochus inornatus Tenison Woods, 1878b: 309–310, pl. 6, figs. 2a–c.—Cairns and Parker, 1992: 20–21, pl. 5, figs. a, d, g–h (synonymy and description).

New Records

Soela: stn 01/84/74, 1, WAM 534–84.

Lady: stn RW96–29, 1, NTM C8087.

Distribution

Western Australia: continental slope south of Cartier Island and west of Browse Island; 302–400 m. Elsewhere: southeastern Australia off Victoria and New South Wales; 146–220 m (Cairns and Parker 1992).

Genus *Oxysmilium* Duchassaing, 1870

Oxysmilium circularis sp. nov.

Figure 2 i–k

Records

Soela: stn 02/82/16, holotype, WAM 102–83; stn

02/82/17, cluster of 9 paratypes, WAM 105–83; stn 02/83/13A, 4 paratypes: 1 (WAM 85–84), 3 (USNM 96990).

Type Locality

18°41'S, 117°54'E (off Port Hedland, WA); 200–204 m.

Description

Corallum elongate-conical, straight to slightly bent, and attached by a slender (PD:GCD = 0.26–0.28), nonreinforced pedicel. Holotype 19.1 mm in calicular diameter, 31 mm in height, and 5.5 mm in pedicel diameter. Calice circular. Theca heavily encrusted with calcareous epifauna, obscuring costae. Septa hexamerally arranged in 5 cycles, the fifth not complete: S1>S2>S3>S4>S5. Holotype contains 66 septa: 5 half-systems with no S5, 5 having 1 pair of S5, and 2 having 2 pairs of S5. S1 slightly exsert (about 1.2 mm), with straight, thickened inner edges reaching to columella. S2 about 4/5 width of the S1, also having straight inner edges. S3 4/5 width of the S2, with straight inner edges. S4 half width of the S3, unless flanked by a pair of S5, in which case they are almost as large as the S3, the S5 being half the width of the S4. Septal faces bear numerous very small, low granules, resulting in almost smooth, planar faces. Fossa deep, containing a papillose columella composed of 1–10 slender, irregularly-shaped pillars.

Remarks

Only one other Recent species is known in this genus, *O. rotundifolia* (Milne Edwards and Haime 1848a), endemic to the western Atlantic at depths of 46–640 m (Cairns 1979). *O. circularis* differs in having a circular calice (that of *O. rotundifolia* is elliptical); S1 that are wider than the S2 (S1 and S2 are equal in width in *O. rotundifolia*); a nonreinforced base (the base of *O. rotundifolia* is often reinforced with rings of exothecal rootlets); and in having fewer septa (66 vs 96+), although larger coralla of *O. circularis* may prove to have a complete fifth cycle.

Distribution

Western Australia: continental slope of northwestern coast off Port Hedland and south of Rowley Shoals; 201–404 m; 9.6°–16.2°C.

Etymology

This species name *circularis* (Latin *circularis*, round) refers to the round calice of this species.

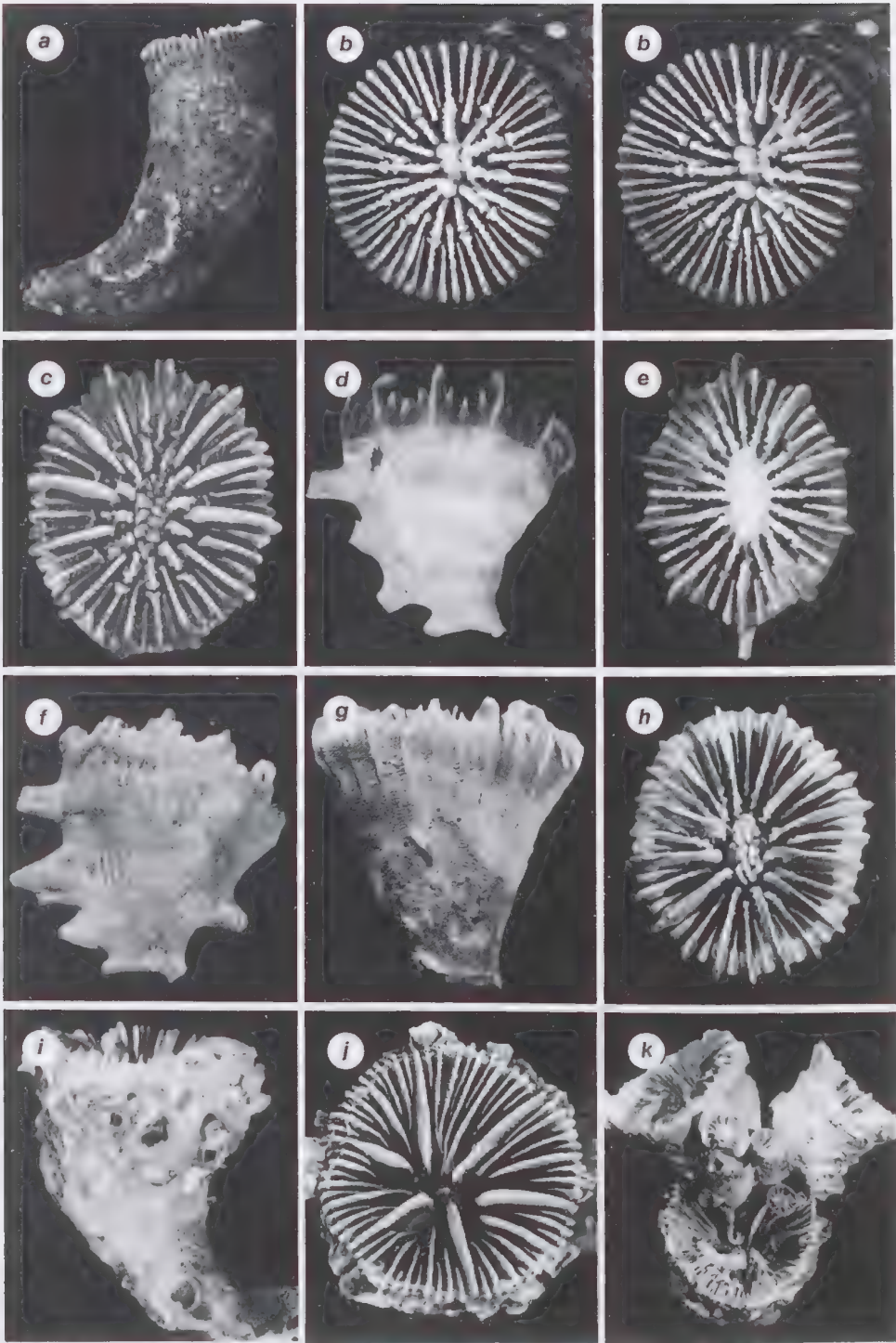


Figure 2 a-c, *Caryophyllia stellula*: a-b, side and stereo calicular views of holotype, $\times 2.0$; c, calicular view of a paratype from a Comet station, SAM H859, $\times 3.6$. d-f, *Caryophyllia (A.) decamera*: d-e, side and calicular views of holotype, $\times 3.1$, $\times 3.6$, respectively; f, paratype, Soela stn 01/84/85, WAM 681-84, side view, $\times 3.1$. g-h, *Crispatotrochus inornatus*, Soela stn 01/84/74, WAM 534-84, side and calicular views, $\times 2.8$. i-k, *Oxysmilia circularis*: i-j, side and calicular views of holotype, $\times 1.9$, $\times 2.2$, respectively; k, Soela stn 02/82/17, WAM 105-83, a cluster of paratypes, $\times 1.1$.

Genus *Trochocyathus* Milne Edwards and Haime, 1848a

***Trochocyathus philippinensis* Semper, 1872**

Trochocyathus philippinensis Semper, 1872: 253, pl. 20, fig. 16.—Cairns and Zibrowius, 1997: 107–108, figs. 10 d–e (synonymy and description).

New Records

Soela: stn 02/82/10A, 7: 4 (WAM 49–84), 3 (USNM 96991); stn 02/82/51, 1, WAM 115–83.

Lady Basten: stn LB5(s), 19, WAM 26–96; stn LB5(t), 1, WAM 454–96.

Distribution

Western Australia: continental shelf of northwestern coast off Port Hedland; 100–154 m. Elsewhere: western Pacific from Ryukyu Islands to Banda Sea; 100–268 m (Cairns and Zibrowius 1997).

***Trochocyathus apertus* Cairns and Zibrowius, 1997**

Caryophyllia (*Premocyathus*) *compressa* – Wells, 1956: F422, fig. 323,3.

Premocyathus compressus – Cairns, 1984: 14 (in part: *Albatross* specimens).—Veron, 1986: 605, black and white fig.

Trochocyathus apertus Cairns and Zibrowius, 1997: 109–110, figs. 11 a–d.

New Records

None.

Remarks

As the synonymy indicates, this species of *Trochocyathus* has been confused with *Premocyathus compressus* Yabe and Eguchi, 1942 by several authors. Although their coralla are quite similar — both species having curved coralla with an open base — *T. apertus* differs in having a papillose (not fascicular) columella and rudimentary P1–2 as well as well-developed P3.

Distribution

Western Australia: Veron (1986) illustrated a specimen from Point Cloates, WA (20–?230 m), which is the only known record from this state. Elsewhere: Philippines and Indonesia; 33–70 m (Cairns and Zibrowius 1997). ?Great Barrier Reef (Veron, 1986).

Genus *Paracyathus* Milne Edwards and Haime, 1848a

***Paracyathus rotundatus* Semper, 1872**

Paracyathus rotundatus Semper, 1872: 253–254, pl.

20, figs. 15a, b.—Faustino, 1927: 72–73, pl. 5, figs. 13–14.—Cairns and Zibrowius, 1997: 115–116, figs 13 d–e.

?*Paracyathus caeruleus* Duncan, 1889: 5, pl. 1, figs. 10–11.

?*Paracyathus merguiensis* Duncan, 1889: 6, pl. 1, figs. 12–14.

New Records

Soela: stn 05/82/22, 1, WAM 53–83; stn 05/82/71, 1, WAM 80–83.

Distribution

Western Australia: continental shelf off Dampier Archipelago; 30–40 m. Elsewhere: western Pacific from South China Sea to Indonesia; 18–66 m (Cairns and Zibrowius 1997); ?Mergui Archipelago (Duncan 1889).

***Paracyathus ?fulvus* Alcock, 1893**

Figure 4 d, g

Paracyathus fulvus Alcock, 1893: 139–140, pl. 5, figs. 2, 2a.

New Records

Soela: stn 01/84/54, 3: 2 (WAM 21–85), 1 (USNM 96993); stn 01/84/109, 1, WAM 693–84.

Redescription

Corallum subcylindrical and squat, the 3 known specimens all firmly attached to the tip of the siphonal canal of a gastropod shell, also encrusting the shell with a thin costate, granular coenosteum as far as 20 mm from the pedicel. Largest Western Australian specimen (WAM 21–85) 12.8 × 11.9 mm in calicular diameter and 10.8 mm in height. Calice circular to slightly elliptical (GCD:LCD = 1.0–1.12). Costae broad (0.8–1.0 mm), slightly convex, and covered with small granules such that 4–7 occur across the width of one costa near the calicular edge. Corallum white except for the S1, which are light brown near calicular edge. Septa hexamerally arranged in 4 complete cycles (48 septa): S1>S2>S4>S3. S1 moderately exsert (up to 2.5 mm), thick, and extend about 2/3 distance to columella. S2 about 1.5 mm exsert and 3/4 width of the S1. S3 1.0 mm exsert and 3/4 width of the S3. S4 as exsert as the S2, each pair of S4 being fused to an S1 at the calicular edge in a lancetted profile; S4 slightly wider than S3. All septa have moderately sinuous inner edges and granular (spinose) septal faces. S1–3 bear 1–4 slender paliform lobes, each progressive cycle of lobes rising slightly higher in the fossa. P4 paliform lobes merge with the P3 adjacent to columella. All paliform lobes bear oblique carinae, merging with the columella toward center of fossa. Fossa of moderate depth, containing a well-

developed papillose columella consisting of many small interconnected irregularly shaped elements.

Remarks

Among the approximately 19 Recent species of *Paracyathus* (Best et al. 1995), only *P. fulvus* has S1 larger than its S2 and a strongly encrusting base. It is not possible to confirm this identification without having examined the holotype in the Calcutta Museum, and thus this identification is considered tentative. This is believed to be the only report of *P. fulvus* subsequent to its original description.

Folkeson (1919) also reported *Paracyathus profundus* Duncan, 1889 from the same station as above, but re-examination of this specimen reveals that it has deteriorated significantly since originally reported. What remains appears to be the corallum of a rhizangiid.

Distribution

Western Australia: continental slope of northwestern coast off Dampier Land; 350–433 m. Elsewhere: Persian Gulf; depth unknown (telegraph cable).

Genus *Stephanocyathus* Seguenza, 1864

Subgenus *Acinocyathus* Wells, 1984

Stephanocyathus (A.) *spiniger* (Marenzeller, 1888)

Stephanotrochus spiniger Marenzeller, 1888: 20–21.

Odontocyathus sexradii – Hoffmeister, 1933: 10, pl. 1, figs. 6–8.

Stephanocyathus spiniger – Veron, 1986: 607, black and white fig.

Stephanocyathus (A.) *spiniger* – Cairns and Parker, 1992: 26–27, pl. 7, figs. g–i (synonymy and description).—Cairns and Zibrowius, 1997: 118–119, fig. 13 f, fig. 14 d.

New Records

Soela: stn 01/84/54, 1, WAM 549–84; stn 01/84/55, 1, WAM 558–84; stn 01/84/120, 4: 2 (WAM 806–84), 2 (USNM 96994); stn 01/84/121, 3, WAM 402–86; stn 01/84/122, 1, WAM 730–84.

Courageous: stn 002, 3: 2 (WAM 25–84), 1 (USNM 96995); stn 023, 1, WAM 29–84.

Distribution

Western Australia: continental slope of northwestern coast from Dampier Land to Port Hedland; 298–535 m; soft (muddy) substrates. Elsewhere: widespread from southwestern Indian Ocean to Japan, including ridges north of New Zealand and the Great Australian Bight off southwestern South Australia (Cairns and Parker 1992; Cairns and Zibrowius 1997).

Stephanocyathus (A.) *explanans* (Marenzeller, 1904)

Stephanotrochus explanans Marenzeller, 1904: 304–307, pl. 18, figs. 19a–b.

Stephanocyathus (A.) *explanans* – Cairns and Keller, 1993: 243–244.—Cairns and Zibrowius, 1997: 119, fig. 14 e (synonymy and description).

New Records

Soela: stn 01/84/51, 1, WAM 541–84; stn 01/84/60, 1, WAM 575–84; stn 01/84/61, 1, WAM 737–84; stn 01/84/71, 1, WAM 536–84; stn 01/84/80, 1, WAM 670–84; stn 01/84/81, 1, WAM 673–84; stn 01/84/116, 2, USNM 96997; stn 01/84/118, 1, WAM 780–84; stn 01/84/121, 1, WAM 792–84.

Courageous: stn 003, 2, WAM 27–84; stn 015, 2, USNM 96996; stn 025, 1, WAM 31–84.

Diamantina: stn 25, 1, WAM 302–83.

Lady: stn RW96–30, 1, NTM C8090.

Distribution

Western Australia: continental slope of western coast from Cartier Island to Rottnest Island; 180–500 m; soft (muddy) substrates. This may be the *Stephanocyathus* species alluded to by Veron (1986: 607) from Rottnest Island. Elsewhere: southwestern Indian Ocean through Indonesia; 183–1016 m (Cairns and Zibrowius 1997).

Genus *Deltocyathus* Milne Edwards and Haime, 1848a

Deltocyathus magnificus Moseley, 1876

Figure 4 a

Deltocyathus magnificus Moseley, 1876: 552–553.—Grygier, 1991: 43, fig. 21G.—Cairns and Parker, 1992: 27–28, pl. 7, figs. j–l, pl. 8, fig. a.—Cairns, 1994: 56, pl. 24, figs. d–e, g–h (synonymy and description).—Cairns and Zibrowius, 1997: 126–127.

Fungiacyathus sp. Veron, 1986: 598, black and white fig.

New Records

Soela: stn 01/84/51, 2, WAM 540–84; stn 01/84/55, 1, WAM 556–84; stn 01/84/60, 3: 2 (WAM 574–85), 1 (USNM 96998); stn 01/84/67, 3, WAM 744–84; stn 01/84/77, 1, USNM 96999; stn 01/84/80, 1, WAM 671–84; stn 01/84/85, 1, WAM 679–84; stn 01/84/91, 2, WAM 688–84; stn 01/84/120, 6, WAM 701– and 807–84; stn 01/84/122, 1, WAM 729–84; stn 02/82/21, 1, WAM 26–83 (figured by Veron, 1986); stn 02/82/27, 1, WAM 35–83; stn 02/82/28, 1, WAM 106–84; stn 02/82/29, 1, WAM 33–83; stn 02/82/31, 1, WAM 434–96; stn 02/82/35, 1, WAM 31–83; stn 02/82/46, 1, WAM 38–83; stn 04/82/8B, 1, WAM 83–83.

Lady: stn RW96–19, 5, NTM C8085.

Courageous: stn 83/25, 1, WAM 107–84; stn 002, 1, WAM 63–84; stn 003, 1, WAM 62–84; stn 004, 1, WAM 65–84; stn 013, 2, WAM 64–84.

Umatoka Maru: stn 6920, 1, WAM 128–84; stn 6921, 1, WAM 147–84; stn 6922, 1, WAM 1024, 85; stn 6926, 1, WAM 104–84.

Surefire: stn 5, 1, WAM 187–92.

Remarks

First reported from Western Australia by Grygier (1991) as the host of a petraroid ascothoracidan crustacean, one additional specimen from *Soela* stn 01/84/120 is reported and figured (Fig 4a) that contains this characteristic crustacean gall. Similar galls have also been reported from this species in the Japan region (Grygier and Nojima 1995).

Distribution

Western Australia: common on continental slope of northwestern coast from Cartier Island to Port Hedland; 260–696 m; 8.2°–9.0°C; soft (muddy) substrates. Elsewhere: western Pacific from Japan to southeastern Australia; 88–1500 m (Cairns and Zibrowius 1997).

Deltocyathus suluensis Alcock, 1902c

Deltocyathus magnificus var. *suluensis* Alcock, 1902c: 20–21.

Deltocyathus suluensis – Cairns and Zibrowius 1997: 125, fig. 16 d (synonymy and description).

New Records

Soela: stn 01/84/60, 1, WAM 576–84; stn 01/84/63, 1, WAM 738–84; stn 01/84/120, 3: 2 (WAM 700–84), 1 (USNM 97000).

Courageous: stn 000 or 001, 1, WAM 67–84; stn 002, 1, WAM 69–84.

Distribution

Western Australia: continental slope of northwestern coast from Dampier Land to Port Hedland; 401–530 m; soft (muddy) substrates. Elsewhere: Philippines; Indonesian region; ridges north of New Zealand; 142–565 m (Cairns and Zibrowius 1997).

Deltocyathus sarsi (Gardiner and Waugh, 1938)

Figure 3 k–l

Fungiacyathus sarsi Gardiner and Waugh, 1938: 201, pl. 7, figs. 17–18 (description).

New Record

Diamantina: stn 45, 1, WAM 1028–79.

Remarks

Among the approximately 20 extant species of

Deltocyathus, 4 have 5 cycles of septa and only 3 frequently reproduce by fragmentation, *D. sarsi* being the only species to have both characters. It differs from *D. suluensis* in having a regenerated corallum and much better developed S5. The single specimen reported herein of 15.1 mm in calicular diameter is thought to be the only record of this species subsequent to its original description.

Distribution

Western Australia: continental shelf of southwestern coast north of Rottnest Island; 80 m. Elsewhere: Maldiv Islands (Kolumadulu Atoll); 44 m (Gardiner and Waugh 1938).

Genus *Heterocyathus* Milne Edwards and Haime, 1848a

Heterocyathus aequicostatus Milne Edwards and Haime, 1848a Figure 3 a–b

Heterocyathus aequicostatus Milne Edwards and Haime, 1848a: 324, pl. 10, fig. 8.—Folkeson, 1919: 8–10 (in part: pl. 1, figs. 8–9).—Wells, 1964: 108.—Veron, 1986: 558–559 (in part: color fig., not black and white, which is *Heteropsammia*).—Hoeksema and Best, 1991: 226–230, figs. 1–11 (synonymy, key, and diagnosis).

New Records

Crown of Thorns Survey (1972, 1974): Dampier Archipelago (Rosemary Island and Norbill Bay, 0–5 m), collectively 65 specimens from 6 collections: 58 (WAM 152–, 162–, 163–, and 164–83; 248–, and 262–93) and 7 (USNM 97001).

Other records: South Head, Beagle Bay, beach drift, 28 X 1988, 1, WAM 1056–88; near Keraudren, Western Australia, low tide, IX 1976, 13, WAM 151–83.

Diagnosis

Corallum relatively large (10 mm in GCD) and squat, either free of attachment or encrusting a scaphopod or gastropod shell; primary sipunculid efferent pore circular, 2.0–2.2 mm in diameter, usually located aborally, and often lending an asymmetry to corallum. Additional smaller (0.4 mm in diameter) sipunculid pores (previous efferent pores that have been subsequently overgrown by the coral but still retain an open canal through the corallum (Yonge 1975)) also occur on lateral thecal faces. Corallum entirely white. Costae equal in width as well as being approximately equal in width to intercostal furrows. Septa crowded and hexamerally arranged in 4 complete and often an incomplete fifth cycle (48–72 septa): S1>S2>S4>S3 or S1>S2>S3>S5>S4, depending on the presence of pairs of S5 in a half-system. Outer edges of septa slope inward toward

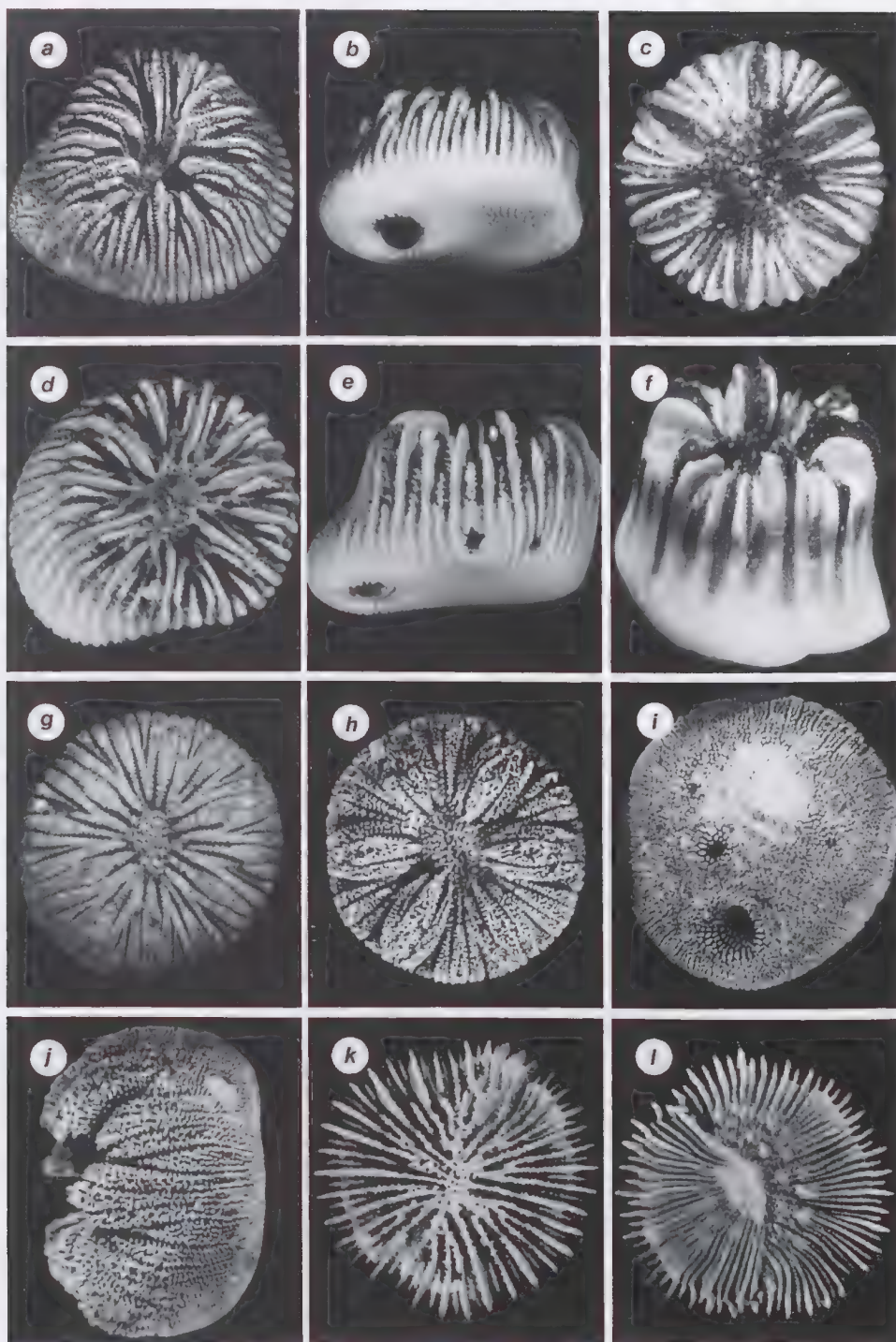


Figure 3 a-b, *Heterocyathus aequicostatus*, Rosemary Island, WAM 263-93, oblique and side views, $\times 2.9$. c, f, *H. sulcatus*, Lady Basten stn LB1b, WAM 8-96, calicular and side views, $\times 5.2$. d-e, *H. alternatus*, Lady Nora Flats, WAM 435-96, calicular and side views, $\times 5.2$. g-j, *H. hemisphaericus*: g, holotype, BMNH, calicular view, $\times 4.1$; h-j, calicular, basal, and side views of syntype of *Spongiocyathus typicus*, SMNH 4756, $\times 4.1$, $\times 4.4$, $\times 4.8$, respectively. k-l, *Deltocyathus sarsi* from Rottnest Island, WAM 1028-79, calicular and basal views, both $\times 3.0$.

columella, not projecting outward. Septa adjacent to S1 (either S4 or S5) almost as exsert as the S1–2 but less wide and porous. Multiple paliform lobes often present on all septa; columella trabecular.

Remarks

Heterocyathus aequicostatus is the most commonly collected and reported of the four congeners, which is also true for the Western Australian region. According to Hoeksema and Best (1991), it has 15 junior synonyms. All four species co-occur and are sometimes difficult to distinguish, but *H. aequicostatus* differs by having closely packed septa, a white corallum, and relatively porous higher cycle septa.

Distribution

Western Australia: continental shelf of western coast from Beagle Bay to Shark Bay (Veron 1986); 0–20 m. Elsewhere: Indo-West Pacific; depth range not known.

Heterocyathus alternatus Verrill, 1865

Figure 3 d–e

Heterocyathus alternata Verrill, 1865: 149.

Heterocyathus alternatus – Folkeson, 1919: 10–11, pl. 1, figs. 10–11.—Hoeksema and Best, 1991: 230–231, figs. 12–18 (synonymy, diagnosis, key).

New Records

Rosemary Island, Dampier Archipelago (Norbill Bay and Lady Nora Flats), 0–5 m, 13: 11 (WAM 435–96 and 480–96), 2 (USNM 97002); Mermaid Sound, Dampier Archipelago, Conzinc Island, 7–9 m, 1, WAM 340–88.

Remarks

Heterocyathus alternatus is most similar to *H. aequicostatus*, but can be distinguished by having: less crowded septa, the S4 of which are angled toward their adjacent S3 giving the septa of the calice a stellate aspect; and having more solid and taller S4, appearing as small lobes fused to the sides of the S1–2. Hoeksema and Best (1991) provided a key to the species of this genus.

Distribution

Western Australia: known only from Dampier Archipelago; 0–9 m. Elsewhere: Indo-West Pacific; depth range not known (Hoeksema and Best 1991).

Heterocyathus sulcatus (Verrill, 1866)

Figure 3 c, f

Stephanoseris sulcata Verrill, 1866: 48.

Heterocyathus pulchellus Rehberg, 1892: 8–9, pl. 1, figs. 7a–b.

Heterocyathus aequicostatus – Folkeson, 1919: 8–10 (in part: pl. 1, figs. 4–7).—Hoeksema and Best, 1991: 231–233, figs. 19–23 (synonymy, key, and diagnosis).

New Records

Soela: 05/82/unknown station number, off Port Hedland, depth unknown, 2, USNM 97003.

Dorothea: 65 mi (=104 km) NE of Adele Island, 73 m, 1, WAM 143–83; 20 mi (=32 km) north of Adele Island, 73 m, 3, WAM 327–89.

Kunmunyah: stn BG47, 1, NTM C8014.

Lady Basten: stn LB1b(s), 2, WAM 8–96; stn LB5(s), 1, WAM 33–96.

Other records: Gulf of Carpentaria, "Gulf" stn 18, 3, USNM 93201.

Remarks

Heterocyathus sulcatus is one of three species in this genus recognized by Hoeksema and Best (1991), differentiated from the other two by having a relatively smaller corallum, only 48 septa, and a darkly pigmented (black or black-brown) fossa (septal, pali and columella). Alternating costae are also commonly pigmented.

Distribution

Western Australia: continental shelf of northwestern coast from Adele Island to Dampier Archipelago; 11–150 m. Elsewhere: northeastern Australia from Peron Islands, Northern Territory (reported herein) to Princess Charlotte Bay, Qd.; off Sri Lanka; Indonesia (Hoeksema and Best 1991); 17–36 m.

Heterocyathus hemisphaericus Gray, 1849

Figure 3 g–j

Heterocyathus hemisphaerica Gray, 1849: 77, pl. 2, figs. 3–4.

Psammoseris hemispherica – Milne Edwards and Haime, 1851: 127.—Wells, 1956: F436.—Veron, 1986: 610, black and white fig.

Spongiocyathus typicus Folkeson, 1919: 11–12, pl. 1, figs. 12–15.

New Records

Soela: stn 1/66, 1, WAM 355–90; stn 05/82/22, 1, WAM 52–83.

Other records: stn SB3, 24°54'S, 113°17.7'E, 23 m, 1, WAM 698–81; stn SB70, 25°31.8'S, 113°32.8'E, 11 m, 1, WAM 1012–81; stn eWm, Withnell Bay, Dampier Archipelago, depth unknown, 1, WAM 380–88; stn B5, 28°46.6'S, 114°04'E, 46 m, 1, WAM 880–89; stn H7, 28°49.5'S, 113°56.3'E, 37 m, 1, WAM 881–89; stn T8, 20°58'S, 115°55'E, 12 m, 1, WAM 354–90; stn E5, Mermaid Shoal, Dampier Archipelago, depth unknown, 1, WAM 29–85; stn

PAe, Mermaid Shoal, 9 m, 3, WAM 337–88; stn PE4–7, Mermaid Shoal, 13–16 m, 2, WAM 363– and 365–88; stn pAs, Mermaid Shoal, 7–9 m, 1, WAM 339–88; Norbill Bay, Dampier Archipelago, 1–2 m, 1, USNM 97004; 28°39.5'S, 113°49.5'E, 38 m, 4, WAM 139–83; *Peron* stn B159, Shark Bay, 1, WAM 228–93; Shark Bay, depth unknown, 1, USNM 97006; east of Sholl Island, Passage Islands, 12 m, 3, USNM 97005.

Remarks

Vaughan and Wells (1943) and Wells (1956) defined the suborder Dendrophylliina as having porous septa and theca (a synapticulotheca), and, believing *Psammoseris hemisphaerica* to have both porous septa and costae, placed it as a genus in that suborder. However, examination of the types of *H. hemisphaerica* (BMNH) and *Spongiocyathus typus* (SMNH 4753–56) reveals that, whereas their septa are highly porous, their costae and theca are solid, much like that of a turbinoliid. I therefore agree with Hoeksema and Best (1991) that *Psammoseris hemisphaerica* must be returned to the Caryophylliidae and the genus *Psammoseris* placed as a junior synonym of *Heterocyathus*. It is ironic that Folkson (1919) correctly placed *Psammoseris* in synonymy with *Heterocyathus*, but did not realize that his new genus *Spongiocyathus*, which he considered as a caryophylliid, was a junior synonym of *Heterocyathus* as well, based on the same species: *Heterocyathus hemisphaericus*.

Heterocyathus hemisphaericus differs from *H. aequicostatus* in having: 48 highly porous septa, only the S4 of *H. aequicostatus* being slightly porous, and usually numbering more than 48; very thick (i.e., 0.9 mm vs 0.15 mm wide) S1; costae that are much wider than the intercostae, composed of elongate spines that originate directly from the theca, not costae that are equal in width to the intercostae and composed of granules that ornament costal ridges, as in *H. aequicostatus*; sipunculid efferent pores and canals opening only on the base of the corallum, those of *H. aequicostatus* opening on the base and edges of the corallum.

Distribution

Western Australia: continental shelf of western coast from Cape Jaubert to Houtman Abrolhos Islands; 2–46 m. Elsewhere: ?South China Sea; depth range not known (Gray 1849).

Genus *Conotrochus* Seguenza, 1864

Conotrochus funiculumna (Alcock, 1902a)

Ceratotrochus (*Conotrochus*) *funiculumna* Alcock, 1902a: 93; 1902c: 11–12, pl. 1, figs. , 6a.

Conotrochus sp. cf. *C. funiculumna* – Cairns and Parker, 1992: 22, fig. 6c, f.

Conotrochus brunneus – Cairns and Parker, 1992: 22 (specimens cited from “southern Western Australia”).

Conotrochus funiculumna – Cairns, 1994: 58–59, pl. 24, fig. i, pl. 25, figs g–l (synonymy and description).—Cairns and Zibrowius, 1997: 127.

New Records

Comet: 204–222 km southwest of Eucla, 240–245 m, 14 I 1989, 12, SAM H860–863.

Lady: stn RW96–18, 1, NTM C8076.

Remarks

This species was alluded to as *Conotrochus brunneus* by Cairns and Parker (1992), based on the SAM specimens documented above.

Distribution

Western Australia: known only from Great Australian Bight off Eucla and Point Dover; south of Cartier Island; 240–280 m. Elsewhere: western Pacific from Japan through Indonesia; Hawaiian Islands; Victoria, Australia; 88–616 m (Cairns and Zibrowius 1997).

Genus *Paraconotrochus* Cairns and Parker, 1992

Paraconotrochus zeidleri Cairns and Parker, 1992

Paraconotrochus zeidleri Cairns and Parker, 1992: 21–22, pl. 5, fig. i, pl. 6, figs. a–b (description).—Cairns and Zibrowius, 1997: 130.

New Records

Soela: stn 01/84/24, 2, NMV F78392; stn 01/84/77, 1, WAM 528–84; stn 01/84/78, 1, WAM 746–84; stn 01/84/79, 1, USNM 97007.

Distribution

Western Australia: continental slope of northwestern coast from Browse Island to Port Hedland; 304–484 m. Elsewhere: Tasmania; New South Wales; Indonesia; Admiralty Islands; 351–558 m.

Genus *Desmophyllum* Ehrenberg, 1834

Desmophyllum dianthus (Esper, 1794)

Madrepora dianthus Esper, 1794: pl. 69, figs. 1–3.

Desmophyllum cristagalli – Hoffmeister, 1933: 8–9, pl. 2, figs. 1–4.—Cairns and Parker, 1992: 28–29, pl. 8, fig. b–c (description).

Desmophyllum dianthus – Cairns, 1994: 26–27, pl. 9, figs. a–d (synonymy and description).—Cairns and Zibrowius, 1997: 131, figs 17 g–h.

New Record

Longva III: stn “2”, 1, SAM.

Distribution

Western Australia: western Great Australian Bight; 963–1011 m. Elsewhere: virtually cosmopolitan, except for continental Antarctic and boreal North Pacific, but including southeastern Australia; 35–2460 m (Cairns and Parker 1992).

Genus *Thalamophyllia* Duchassaing, 1870

Thalamophyllia tenuescens (Gardiner, 1899)

Desmophyllum tenuescens Gardiner, 1899: 161–162, pl. 19, figs. 1a–b.

Thalamophyllia tenuescens – Cairns, 1995: 78, pl. 21, figs. g–i (description).—Cairns and Zibrowius, 1997: 133, figs. 17 d–e.

New Records

Stn 16, 13°56'S, 125°37'E (Cassini Island), "SCUBA depth", 18 VIII 1991, 1, WAM 436–96 (in part, attached to base of *Rhizopsammia verrilli*); stn C71, NE of Leo Island, Easter Group, Houtman Abrolhos Islands, 38 m, 1 IX 1972, 4 corallites, WAM 437–96.

Distribution

Western Australia: continental shelf off Cassini Island, Kimberley, and Houtman Abrolhos Islands; 38 m. Elsewhere: western Pacific from Philippines to Kermadec Islands, including off Queensland; 8–315 m (Cairns and Zibrowius 1997).

Genus *Asterosmilia* Duncan, 1867

Asterosmilia marchadi (Chevalier, 1966)

Dasmosmilia marchadi Chevalier, 1966: 944–949, pl. 5, figs. 3–4.

Asterosmilia marchadi – Zibrowius, 1980: 141–142, pl. 74, figs. A–K (synonymy and description).—Cairns and Zibrowius, 1997: 131–132, figs. 17 a–b.

New Records

Lady Basten: stn LB5(s), 11, WAM 30–96; stn LB5(t), 1, WAM 20–96.

Distribution

Western Australia: known only from continental shelf off Port Hedland; 150–160 m. Elsewhere: cosmopolitan in tropical seas, except for eastern Pacific; 32–229 m (Cairns and Zibrowius 1997).

Genus *Rhizosmilia* Cairns, 1978

"Rhizosmilia" multipalifera sp. nov.

Figure 4 b–c, e–f

Paracyathus porphyreus – Folkeson, 1919: 12–13, figs. 16–17.

Records

Sprightly: stn 41M, holotype and 2 paratype colonies, WAM 129–83; stn 19M, 1 paratype colony, WAM 127–83; stn 20M, 1 paratype corallite, WAM 132–83; stn 30M, 1 paratype colony, USNM 97008; stn 33M, 1 paratype colony, WAM 360–79; stn 34M, 1 paratype colony, WAM 135–83; stn 40M, 1 paratype colony, USNM 97009; .

Diamantina: stn 55, 1 paratype colony, WAM 242–93; stn 76, 1 paratype corallite, WAM 148–83; stn 208, 1 paratype colony, WAM 226–93.

Other records: Cape Jaubert, 45 mi (72 km) WSW, 66 ft. (20 m), 2 paratypes, SMNH 223 (*Paracyathus porphyreus* of Folkeson 1919).

Type Locality

30°16.8'S, 114°39.6'E (Jurien Bay), WA; 82 m.

Description

Encrusting colonies of up to 35 corallites, each corallite budding from a thin common basal coenosteum. Corallites cylindrical: up to 9.6 mm in GCD and 12 mm in height. Corallite base polycyclic, composed of concentric rings of hollow chambers formed by exothecal dissepiments covering raised costae. Calices elliptical to elongate in cross section: GCD:LCD = 1.1–1.6. Theca often heavily encrusted with calcareous epifauna; costae well developed only near calicular edge as thin ridges. Small corallites white, but larger corallites bear a brown pigmentation on theca near calicular edge. Septa hexamerally arranged in 4 cycles between a GCD of 5–8 mm; larger corallites have additional pairs of S5. S1–2 about 1.1 mm exsert, having slightly sinuous inner edges that extend about half distance to columella. Each S1–2 bears 1–3 small paliform lobes positioned low in fossa near the columella. S3 about 0.9 mm exsert and 3/4 width of the S1–2, each bearing one large paliform lobe that rises higher in the fossa than the P1–2. S4 about 3/4 width of the S3, having lacinate inner edges. If pairs of S5 are present, the flanked S4 bears a P4. Sparse endothecal dissepiments present. Fossa deep, containing a well-developed trabecular columella.

Remarks

Among the six previously described species in the genus, *R. multipalifera* is most similar to *R. sagamiensis* (Eguchi, 1968), but differs by having well-developed paliform lobes before the S1–2 as well as the S3. In this character *R. multipalifera* differs from all other *Rhizosmilia* and is only tentatively placed in the genus.

Distribution

Western Australia: continental shelf of southwestern coast from Cape Jaubert to north of Perth; 11–165 m.

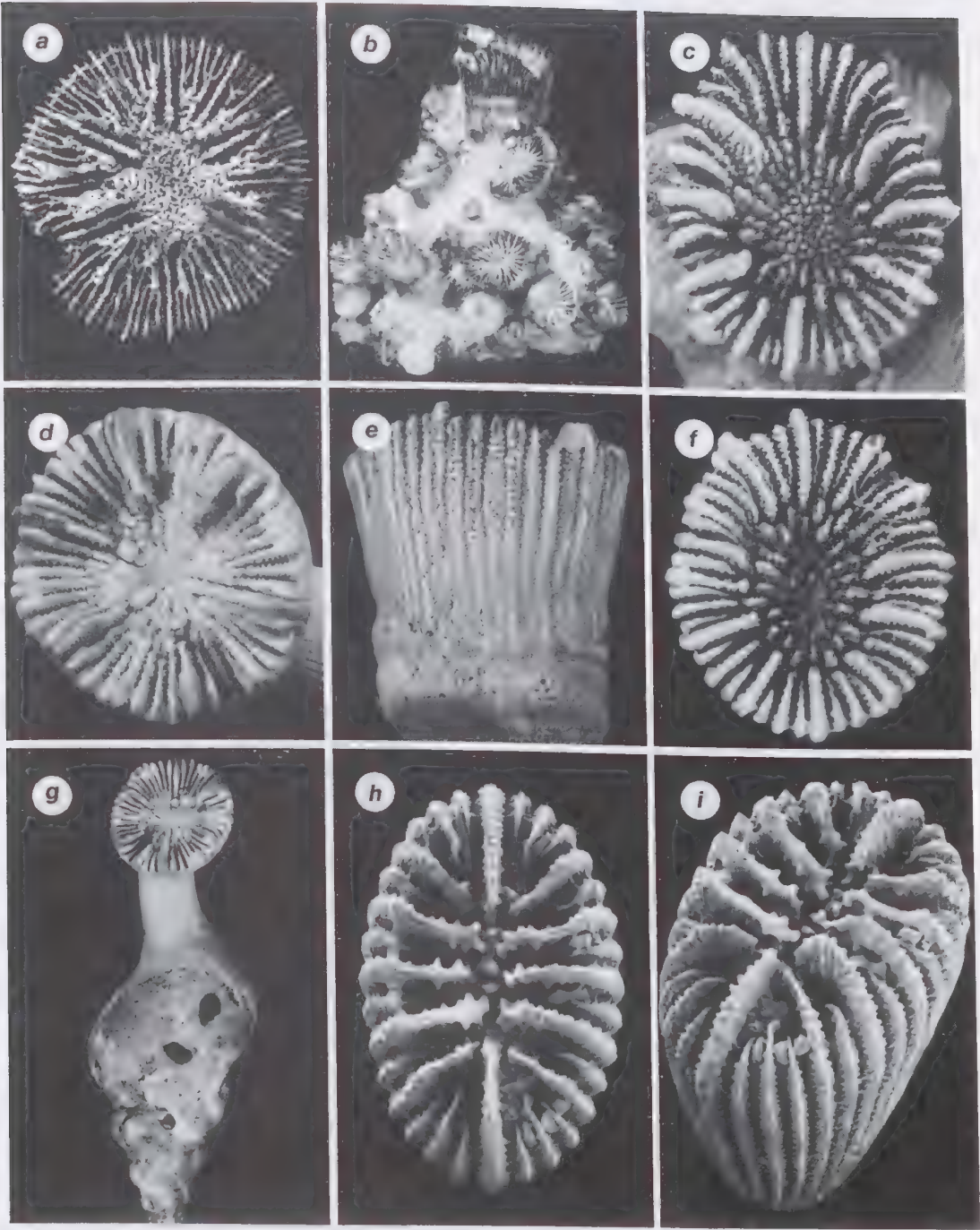


Figure 4 a, *Deltocyathus magnificus*, Soela stn 01/84/120, WAM 701-84, columella deformed by ascothoracidan crustacean gall, x 1.7. b-c, *"Rhizosmilia" multipalifera*: b, paratype colony, Sprightly stn 41M, WAM 129-83, x 1.5; c, calice of holotype, x 7.3; e-f, *Paracyathus porphyreus* of Folkeson (1919), SMNH 223, side and calicular views, x 8.3. d, g, *Paracyathus ?fulvus*, Soela stn 01/84/54, WAM 21-85, calicular view and corallum as attached to gastropod, x 4.4, x 1.7, respectively. h-i, *Trematotrochus verconis*, west of Eucla, USNM 85714, calicular and oblique views, x 19.

Etymology

The species name *multipalifera* (Latin *multus*, many + *paliferus*, bearing stakes (pali)) refers to the numerous paliform lobes in this species.

Genus *Solenosmilia* Duncan, 1873

Solenosmilia variabilis Duncan, 1873

Solenosmilia variabilis Duncan, 1873: 328, pl. 42, figs. 11–18.—Hoffmeister, 1933: 14, pl. 4, fig. 7.—Cairns and Parker, 1992: 29–30, pl. 8, figs. d–e (diagnosis).—Cairns, 1995: 82, pl. 23, figs. d–e (synonymy).

New Records

Longva III: stn "1", SAM; stn "2", SAM.

Distribution

Western Australia: western Great Australian Bight; 963–1011 m. Elsewhere: widespread in Atlantic and Indian Oceans; New Zealand region; southeastern Australia; 220–2165 m (Cairns 1995).

Family Turbinoliidae Milne Edwards and Haime, 1848a

Genus *Trematotrochus* Tenison Woods, 1879

Trematotrochus verconis Dennant, 1904 Figures 4 h–i, 5 a–c

Trematotrochus verconis Dennant, 1904: 5–6, pl. 1, fig. 4a.—Cairns and Parker, 1992: 30–31, pl. 9, figs. a, e (synonymy and description).

?*Trematotrochus lateroplenus* – Wells, 1942: 95–96.

New Records

Sprightly: stn 28M, 1, WAM 361–79.

Other records: Verco collection, 146 km west of Eucla, 148 m, III 1912, 4, including SEM stub 856, USNM 85714.

Remarks

These small specimens indicate that at a GCD of 3.5–3.8 mm the total number of septa increases from 32 to 40.

Although not examined, the Miocene fossil reported by Wells (1942) from the Langley Park Bore may be this species.

Distribution

Western Australia: off Dongara and Eucla, southwestern coast; 148–183 m. Elsewhere: South Australia; 73–101 m (Cairns and Parker 1992).

Genus *Conocyathus* d'Orbigny, 1849

Conocyathus zelandiae Duncan, 1876 Figure 5 d–h

Conocyathus zelandiae Duncan, 1876: 431, pl. 38, figs.

1–3.—Wells, 1964: 112–114 (part).—Cairns, 1995: 83–84, in part: pl. 23, figs. f–i (not specimens from *Alpha Helix* stations) (synonymy and description).—Not Cairns and Zibrowius, 1997: 140–141 (=C. *gracilis*).

Not *Trematotrochus zelandiae* – Folkesson, 1919: 14 (=C. *gracilis*).

Turbinolia australiensis Gardiner, 1939: 332–333, pl. 21, figs. 1–2.

New Records

Espirito Santo: stn E68–743, 1, AMS G15361.

Other records: Stn Cwc, Withnell Bay, Burrup Peninsula, Dampier Archipelago, 4 m, 1 (SEM stub 854), WAM 379–88; Verco collection, King George Sound, 22–26 m, 10: 2, including SEM stub 520 (USNM 85713); 8 (SAM H502).

Distribution

Western Australia: King George Sound and Dampier Archipelago; 4–137 m. Elsewhere: Persian Gulf; ?New Zealand; New South Wales; 130 m.

Conocyathus gracilis sp. nov.

Figures 5 i, 6 a–d

Trematotrochus zelandiae – Folkesson, 1919: 14.

Conocyathus zelandiae – Wells, 1964: 113–114 (in part).—Cairns, 1995: 83 (in part: specimens from *Alpha Helix* stations).—Cairns and Zibrowius, 1997: 140–141.

Records

Soela: stn 01/79/unnumbered, holotype (SEM stub 855), WAM 31–85.

Alpha Helix: stn M14, 7 paratypes, USNM 80852; KARUBAR: stn 44, 4 paratypes, USNM 97320; stn 86, 1 paratype, MNHN.

Other records: off Broome, from stomach of fish, 5 paratypes, SMNH 148 (Mjoberg 1911 collection, *T. zelandiae* of Folkesson 1919).

Type Locality

19°34.5'S, 116°08'E (off Glomar Shoal, NW of Dampier Archipelago); 101 m.

Description

Corallum elongate, slender, and very small, the largest specimen (holotype) 1.55 mm in calicular diameter and 4.75 mm in height. Calice circular, with a H:D ratio of 3.1. All costae (C1–3) equal in width (70–80 µm) and separated by broad intercostal regions 100–125 µm wide. C1–2 extend to base, whereas C3 originate 0.85–1.0 mm above base, and incipient C4 just begin to form on holotype at a height of 4.6 mm. C4 do not correspond to septa. Intercostal region of lower

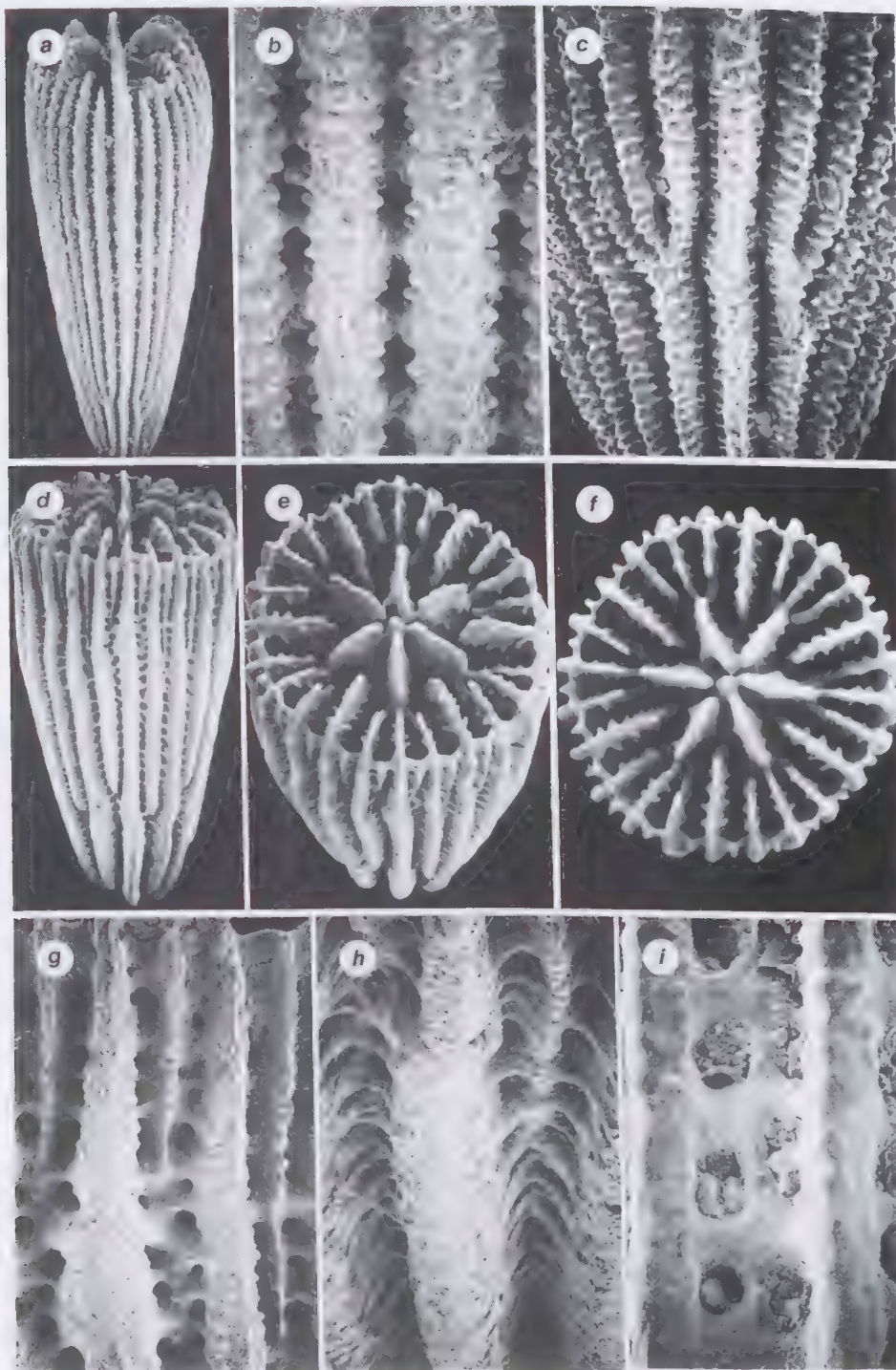


Figure 5 a-c, *Trematotrochus verconis*, west of Eucla, USNM 85714: a, edge view, $\times 12.6$; b, costae and intercostal perforations, $\times 76$; c, trifurcation of higher cycle costae, $\times 53$. d-h, *Conocyathus zelandiae*, Dampier Archipelago, WAM 379-88: d-f, side, oblique, and calicular views, $\times 23$, $\times 30$, $\times 36$, respectively; g, upper theca showing supernumerary costae, $\times 97$; h, enlargement of intercostal pits, $\times 150$. i, *Conocyathus gracilis*, holotype, intercostal pits, $\times 150$.

half of corallum bears a unilinear row of shallow circular to slightly elliptical pits, each about 50 μm in diameter. In upper half of corallum, pits arranged in 2 staggered rows, separated by a thecal midline (Figure 6d). Septa hexamerally arranged in 3 complete cycles ($S1 > S2 > S3$). S1 about 0.22 mm exsert, having straight axial edges that extend about half distance to columella in upper fossa but join to the columella lower in fossa. S2 equally exsert and about 3/4 width of the S1, each bearing a broad, low paliform lobe the inner edge of which fuses to the columella. S3 relatively narrow (about 0.1 mm wide), the upper edges of each pair that flank an S2 fusing to the S2 at calicular edge (forming small lancets) and axial edges of each S3 angled toward and fusing to its adjacent S2 via 2 or 3 trabecular processes. Fossa of moderate depth; columella a solid central fusion of inner edges of S1 and P2.

Remarks

Conocyathus gracilis is similar to and has been confused with *C. zelandiae*, but is distinguished by having a smaller, narrower corallum (GCD max. 1.7 mm and H:D = 3.1 vs GCD max. 3.4 mm and H:D = 1.8); having much less exsert P2 (those of *C. zelandiae* extend above the calicular edge); having only 24 costae, the C4 of *C. zelandiae* beginning to form at a height of 1.9–2.7 mm; having broader intercostal region than costae, the reverse being true for *C. zelandiae*; and in having uniformly wide C1–2 that do not change width at the origin of the C3.

Distribution

Western Australia: known only from continental shelf of northwestern coast off Broome and Glomar Shoal; 101 m. Elsewhere: Arafura Sea (off Arnhem Land, Northern Territory); 22–291 m.

Etymology

The species name *gracilis* (Latin *gracilis*, slender) alludes to the slender corallum of this species, which helps to distinguish it from *C. zelandiae*.

Genus *Alatotrochus* Cairns, 1994

Alatotrochus rubescens (Moseley, 1876)

Platyrochus rubescens Moseley, 1876: 553.

Sphenotrochus rubescens – Moseley, 1881: 157–159, pl. 6, figs 8, 8a.

Alatotrochus rubescens – Cairns, 1994: 68–69, pl. 29, figs g–l (synonymy); 1995: 84, pl. 24, figs. a–b.—Cairns and Zibrowius, 1997: 141–142, fig. 18 h.

New Records

Lady: stn RW96–17, 3: 2 (NTM C8069 and C8074),

1 (USNM 98515); stn RW96–18, 1 (NTM); stn RW96–19, 1 (NTM C8084).

Distribution

Western Australia: south of Cartier Island; 180–350 m. Elsewhere: western Pacific from Japan to southern Norfolk Ridge; 187–751 m (Cairns and Zibrowius 1997).

Genus *Idiotrochus* Wells, 1935

Idiotrochus kikutii (Yabe and Eguchi, 1941)

Placotrochides kikutii Yabe and Eguchi, 1941: 104.

Idiotrochus kikutii – Cairns, 1989: 36–37, pl. 18, figs. a–b, d–h (synonymy and description); 1994: 69, pl. 30, figs. a–d.—Cairns and Zibrowius, 1997: 148–149.

New Record

Soela: stn 02/82/13A, 3, WAM 90– and 96–84.

Distribution

Western Australia: continental slope of northwestern coast off Port Hedland; 201 m. Elsewhere: western Pacific from Japan through Indonesia; 97–645 m (Cairns and Zibrowius 1997).

Genus *Notocyathus* Tenison Woods, 1880

Notocyathus venustus (Alcock, 1902b)

Citharocyathus venustus Alcock, 1902b: 119.

Notocyathus venustus – Cairns, 1989: 27–28, pl. 12, figs. c–h (synonymy and description); 1994: 64, pl. 27, figs. k–l.—Cairns and Zibrowius, 1997: 143.

New Records

Soela: stn 01/79/unnumbered, 2, WAM 32–85.

Umataka Maru: stn 6921, 10: 7 (WAM 150–84 and 325–89), 3 (USNM 97010); stn 6927, 1, WAM 103–84.

MV Kos 2: stn K67–182, 14°12'S, 123°02'E, 194 m, 1, AMS G15353.

Lady: stn RW96–17, 1, NTM C8072.

Distribution

Western Australia: northwestern coast from Cartier Island to off Glomar Shoal; 90–300 m. Elsewhere: western Pacific from southern Japan through Indonesia; 70–555 m (Cairns and Zibrowius 1997).

Genus *Tropidocyathus* Milne Edwards and Haime, 1848a

Tropidocyathus lessonii (Michelin, 1842)

Flabellum Lessonii Michelin, 1842: 119.

Tropidocyathus lessonii – Cairns, 1989: 33–34, pl. 16, figs. d–l (synonymy and description); 1994: 67,

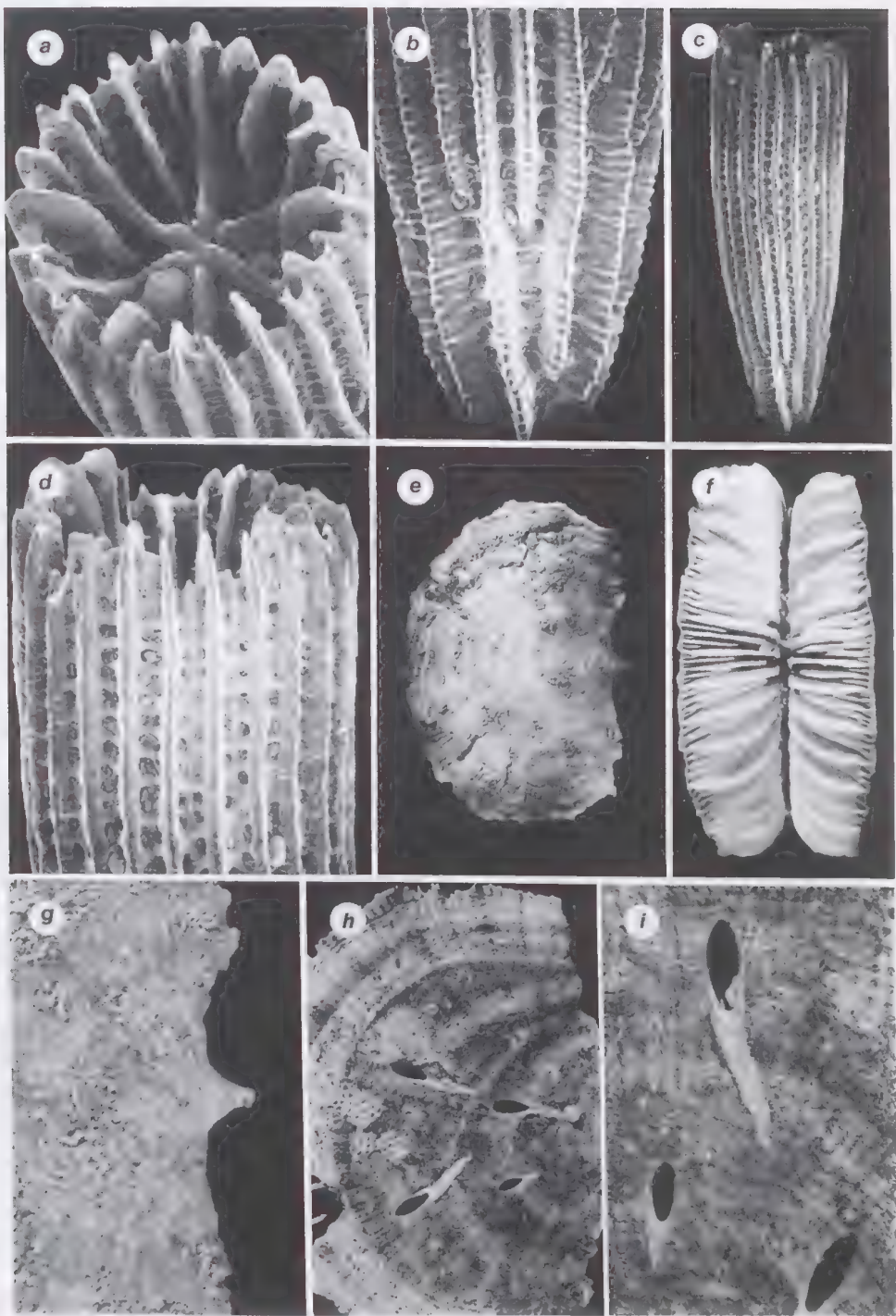


Figure 6 a-d, *Conocyathus gracilis*, holotype: a, oblique calicular view, x 37; b, base of corallum showing independent costal insertion, x 44; c, side view of corallum, x 15; d, intercostal pits, x 37. e-i, *Flabellum folkesoni*, e-g, holotype: e-f, side and calicular views, x 1.2, x 1.4, respectively; g, enlargement of pedicel and adjacent thecal edges, x 3.0; h-i, *Lady Basten* stn LB5(s), WAM 27-96, specimen infested with acrothoracican cirripedes, x 2.9, x 6.5, respectively.

pl. 29, figs. a–b.—Cairns and Zibrowius, 1997: 146–147.

New Records

Diamantina: stn 185, 1, WAM 175–83.

Lady Basten: stn LB5(s), 1, WAM 29–96.

Espiritu Santo: stn E68–743, 2, AMS G15362.

Other records: Port Essington, Cobourg Peninsula, Northern Territory, 1, NTM C8037.

Distribution

Western Australia: from Port Hedland to off Point Cloates; 137–160 m. Elsewhere: Indo-West Pacific (southwestern Indian Ocean to southern Japan); 50–421 m (Cairns and Zibrowius 1997).

Tropidocyathus labidus Cairns and Zibrowius, 1997

"Tropidocyathus" labidus Cairns and Zibrowius, 1997: 148, figs. 20 a–g.

New Records

Umataka Maru: stn 6921, 4, WAM 145, and 151–84; stn 6930, 1, USNM 97011.

Distribution

Western Australia: continental slope of northwestern coast from Browse Island to Rowley Shoals; 300–380 m. Elsewhere: Indonesia; Ryukyu Islands; 206–425 m (Cairns and Zibrowius 1997).

Genus *Cyathotrochus* Bourne, 1905

Cyathotrochus pileus (Alcock, 1902a)

Trochocyathus pileus Alcock, 1902a: 96–97.

Tropidocyathus pileus – Cairns, 1989: 34–35, pl. 17, figs. a–h (synonymy and description); 1994: 68, pl. 29, figs. d–5; 1995: 91, pl. 28, figs. a–c.

"Tropidocyathus" pileus – Cairns and Zibrowius, 1997: 147–148, figs. 19 h–i.

New Records

Soela: stn 01/84/54, 2, WAM 267– and 268–93; stn 01/84/55, 3: 2 (WAM 559–84), 1 (USNM 97012); stn 01/84/74, 2, WAM 532–84.

Umataka Maru: stn 6921, 2, WAM 144–84.

Franklin: stn GAB042, 1, SAM H873.

Lady Basten: stn LB8(t), 1, WAM 49–96.

Distribution

Western Australia: continental slope of northwestern coast from Browse Island to Rowley Shoals; Great Australian Bight; 234–348 m. Elsewhere: Indo-West Pacific (southwestern Indian Ocean to Japan, including Queensland and Norfolk Ridge); 123–522 m (Cairns and Zibrowius 1997).

Genus *Deltocyathoides* Yabe and Eguchi, 1932

Deltocyathoides orientalis (Duncan, 1876)

Deltocyathus orientalis Duncan, 1876: 431, pl. 38, figs. 4–7.

Peponocyathus orientalis – Veron, 1986: 608.

Peponocyathus australiensis – Cairns, 1989: 29, 30–32, pl. 14, figs. d–j, pl. 15, figs. a–d (synonymy and description).—Cairns and Parker, 1992: 39–40, pl. 13, figs. c–d.—Cairns, 1994: 64–65, pl. 28, figs. c–f, pl. 41, fig. i.

Deltocyathoides orientalis – Cairns and Zibrowius, 1997: 144–145.

New Record

Umataka Maru: stn 6920, 3, WAM 326–89.

Distribution

Western Australia: south of Rowley Shoals; 260 m. Elsewhere: Indo-West Pacific (southwestern Indian Ocean to Japan, including South Australia and Queensland); 44–635 m (Cairns and Zibrowius 1997).

Superfamily Flabelloidea Bourne, 1905

Family Guyniidae Hickson, 1910

Genus *Guynia* Duncan, 1872

Guynia annulata Duncan, 1872

Guynia annulata Duncan, 1872: 32, pl. 1, figs. 1–8.—Cairns, 1989: 42–43, pl. 21, fig. f, pl. 22, figs. a–e (synonymy and description).—Cairns and Parker, 1992: 42–43, pl. 14, figs. g–h.—Cairns and Zibrowius, 1997: 150.

New Record

Espiritu Santo: stn E68–743, 3, AMS G15273.

Distribution

Western Australia: known only from continental shelf near Glomar Shoal; 137 m. Elsewhere: cosmopolitan in tropical and warm temperate regions, except for eastern Pacific, including off South Australia; 28–653 m (Cairns and Zibrowius 1997).

Family Flabellidae Bourne, 1905

Genus *Flabellum* Lesson, 1831

Subgenus *Flabellum* Lesson, 1831

Flabellum (F.) *magnificum* Marenzeller, 1904

Flabellum magnificum Marenzeller, 1904: 276–277, pl. 17, fig. 13.—Cairns, 1989: 50–51, pl. 25, figs. a–j (synonymy and description).—Grygier, 1991: 43, fig. 21H.—Cairns, 1994: 72, pl. 31, figs. j–l.—Cairns and Zibrowius, 1997: 151–152.

New Records

Soela: stn 02/82/17, 1, WAM 23–83; stn 02/82/18, 1, WAM 24–83; stn 02/82/31, 1, WAM 29–83; stn 02/82/43, 1, WAM 42–83; stn 02/82/46, 1, WAM 43–83; 01/84/54, 1, WAM 438–96; stn 01/84/59, 1, WAM 572–84; stn 01/84/60, 1, WAM 573–84; stn 01/84/67, 13: 8 (WAM 769–84), 5 (USNM 97013); stn 01/84/71, 1, WAM 537–84; stn 01/84/77, 1, WAM 525–84; stn 01/84/119, 2, WAM 784–84; stn 01/84/121, 1, WAM 401–86; stn 01/84/122, 2: 1 (WAM 728–84), 1 (USNM 97014); stn 04A/82/8B, 2, WAM 46–83.

Courageous: stn 003, 3, WAM 40–84; stn 015, 2, WAM 39–84; stn 017, 1, WAM 34–84; stn 018, 2, WAM 35–84; stn 026, 5: 3 (WAM 41–84), 2 (USNM 97015).

Lady: stn RW96–31, 3: 2 (NTM C8092); 1 (USNM 98516).

Distribution

Western Australia: continental slope of northwestern coast from near Browse Island to off Port Hedland; 306–506 m; 7.8°–12.0°C; soft (muddy) substrates. Elsewhere: western Pacific from Japan through Indonesia, and western Sumatra; 225–700 m (Cairns and Zibrowius 1997).

Flabellum (F.) lamellulosum Alcock, 1902a

Flabellum lamellulosum Alcock, 1902a: 105–106.—Cairns, 1989: 52–53, pl. 27, figs. a–l (synonymy and description).—Cairns and Zibrowius, 1997: 152–153, fig. 21 a.

New Records

Soela: stn 02/82/38, 1, WAM 111–83; stn 02/82/41, 1, WAM 40–83; stn 02/82/45, 1, WAM 41–83; stn 01/84/54, 8: 5 (WAM 552–84), 3 (USNM 97017); stn 01/84/55, 1, WAM 554–84; stn 01/84/56, 1, WAM 563–84; stn 01/84/65, 1, WAM 665–84; stn 01/84/66, 1, WAM 667–84; stn 01/84/67, 1, WAM 743–84; stn 01/84/74, 1, USNM 97018; stn 01/84/122, 1, WAM 439–96; stn 04A/82/8A, 2, WAM 45–83; stn 04/82/8C, 1, WAM 44–83.

Courageous: stn 003, 3, WAM 440–96; stn 020, 1, USNM 97016.

Umataka Maru; stn 6930, 1, WAM 261–93.

Lady: stn RW96–18, 13: 10 (NTM C8081), 3 (USNM 98514).

Distribution

Western Australia: continental slope of northwestern coast from south of Cartier Island to Port Hedland; 280–450 m; 9.1°–10.0°C; soft (muddy) substrates. Elsewhere: western Pacific from South China Sea through Indonesia; 187–486 m (Cairns and Zibrowius 1997).

Flabellum (F.) patens Moseley, 1881

Flabellum patens Moseley, 1881: 172 (in part: pl. 6, fig. 15).—Cairns, 1989: 51–52, pl. 26, figs. a–i (synonymy); 1994: 71–72, pl. 31, figs g–i.—Cairns and Zibrowius, 1997: 152, fig. 20 i.

New Record

Lady: stn RW96–18, 1, NTM C8078.

Distribution

Western Australia: continental slope south of Cartier Island; 280 m. Elsewhere: western Pacific from Japan through Indonesia; 204–439 m (Cairns and Zibrowius 1997).

Flabellum (F.) folksoni sp. nov.

Figure 6 e–i

Records

Other records: unknown station “between Shark Bay and Onslow”, coll. W. and W. Poole, 1966, depth not known, holotype (WAM 173–83) and 23 paratypes (WAM 170–83 and 260–93).

Soela: stn 01/18, 1 paratype, WAM 212–92; stn 02/82/9, 5 paratypes: 2 (WAM 98–83), 3 (USNM 97019); stn 04B/82/74, 1 paratype, WAM 609–88; stn 05/82/47, 1 paratype, WAM 62–83.

Lady Basten: stn LB4(s), 1 paratype, WAM 12–96; stn LB5(s), 27 paratypes: 26 (WAM 27–96), 1 (USNM 96586); stn LB5(t), 21 paratypes: 18 (WAM 23–96), 3 (USNM 97020); stn LB6(s), 6 paratypes, WAM 40–96; stn LB6(t), 1 paratype, WAM 38–96.

Type Locality

“Between Shark Bay and Onslow, WA”; depth unknown.

Description

Angle of thecal edges 180°–210°; angle of thecal faces 27°–30°. Corallum robust and dense; one of largest specimens (the holotype) measures 42.3 x 22.5 mm in calicular diameter and 35.6 mm in height. GCD:H = 0.92–1.19. Pedicel short (3.3–3.6 mm) and small (only 1.1–1.2 mm in diameter). Thecal faces flat, usually encrusted with calcareous epifauna, but glisteny (not granular); well-preserved coralla bear thin reddish-brown stripes corresponding to the S1–6. Thecal faces meet in sharp, carinate edges, forming irregular spurs, as in *F. lamellulosum*, which result from successive downward eversions of the two principal costae followed by subsequent retrenchment of the calicular edge. Septa hexamerally arranged in 7 cycles, the seventh only partially complete in the holotype (274 septa); septa formula: S1–4>S5>S6>S7. Inner edges of S1–4 highly sinuous (SSI about 4.0), occurring closely parallel to edges of S1–4 from opposing face. Upper edges of S1–4

notched near calicular edge (SCI only about 4.3). S5 about 2/3 width of S1–4 and thus easily distinguishable from them; only slightly sinuous. S6 about half width of S5, and when present, S7 rudimentary, composed of a series on low spines occurring only near calicular edge of larger specimens. Fossa deep and narrow (1.5–2.0 mm in width), containing a low, crispate columella.

Remarks

Flabellum folkesoni is similar to *F. lamellulosum*, particularly regarding thecal edge angle, edge ornamentation, and septal formula, but can be distinguished by having highly sinuous axial edges of the S1–4, a smaller pedicel, a narrower face angle, a denser corallum, and smaller S5 in relation to the S1–4. *F. folkesoni* is also found in shallower, warmer waters than *F. lamellulosum*.

Flabellum folkesoni might also be confused with *Truncatoflabellum angiosomum*, which occurs in the same region at similar depths, both species being similarly shaped and about the same size. However, *T. angiosomum* can be distinguished by having straight inner edges of the S1–4; a small truncated base flanked by two thecal edge spines; rounded thecal edges; differently shaped septa; and an edge angle that is usually less than 180°.

Characteristically-shaped (Figs 6h–i) acrothoracican cirripede burrows were found in the coralla from four of the stations listed above, some coralla having as many as 14 burrows on one thecal face. Crescent grooves of commensal lumbrinerid polychaetes were also found on coralla from half of the stations listed above (see Zibrowius, Southward and Day 1975).

Distribution

Western Australia: continental shelf of northwestern coast from Rowley Shoals to Onslow Bay and perhaps as far south as Shark Bay; 124–173 m; 19°–22.8°C.

Etymology

This species is named in honour of Folke Folkeson, who described several new azooxanthellate species from Western Australia (Folkeson 1919).

Flabellum (F.) politum Cairns, 1989

Flabellum politum Cairns, 1989: 53–54, pl. 28, figs. a–f (synonymy and description); 1994: 73, pl. 32, figs. a–c.—Cairns and Zibrowius, 1997: 153–154.

New Records

Soela: stn 02/82/10A, 1, WAM 48–84; stn 02/82/13A, 15: 11 (WAM 55–84), 4 (USNM 96588); stn

01/84/85, 1, WAM 682–84; stn 05/82/36, 1, WAM 58–83.

Umataka Maru: stn 6920, 3, WAM 130–84.

Lady Basten: stn LB1b(s), 2, WAM 9–96; stn LB5(s), 59, WAM 25–96; stn LB5(t), 16, WAM 21–96; stn LB6(s), 2, WAM 43–96.

Remarks

Acrothoracican cirripede burrows were present on the theca of specimens from half of the stations reported above, usually with an infestation rate of 2 or 3 per corallum.

Distribution

Western Australia: continental shelf of northwestern coast from south of Scott Reef to Port Hedland; 45–220 m; 23.1° C; soft (muddy) substrates. Elsewhere: Ryukyu Islands through Indonesia; 40–402 m (Cairns and Zibrowius 1997).

Subgenus *Ulocyathus* Sars, 1851

Flabellum (U.) hoffmeisteri Cairns and Parker, 1992

Flabellum hoffmeisteri Cairns and Parker, 1992: 47–48, pl. 16, figs. d–f.—Cairns, 1995: 103–104, pl. 33, figs. g–h (synonymy and description).—Cairns and Zibrowius, 1997: 157–158.

New Records

Soela: stn 01/84/24, 1, NMV F78391; stn 01/84/51, 1, WAM 539–84; stn 01/84/52, 2, WAM 545–84; stn 01/84/53, 2, WAM 568– and 569–84; stn 01/84/59, 2, WAM 570– and 571–84; stn 01/84/63, 1, WAM 740–84; stn 01/84/64, 13: 9 (WAM 582–84), 4 (USNM 96595); stn 01/84/65, 3, WAM 664–84; stn 01/84/66, 3, WAM 666–84; stn 01/84/67, 11: 7 (WAM 745–84), 4 (USNM 96638); stn 01/84/71, 1, WAM 538–84; stn 01/84/77, 2, WAM 523–84; stn 01/84/81, 1, WAM 675–84; stn 01/84/91, 1, WAM 687–84; stn 01/84/116, 3, WAM 698–84; stn 01/84/119, 2, WAM 782– and 783–84; stn 01/84/120, 7, WAM 805–84; stn 01/84/121, 3, WAM 781–84; stn 02/82/17A, 2, WAM 106–83; stn 02/82/35, 1, WAM 110–83; stn 04A/82/8B, 1, WAM 85–83.

Courageous: stn 002, 8, WAM 26–84; stn 003, 8: 6 (WAM 24–84), 2 (USNM 96591); stn 004, 1, WAM 37–84; stn 015, 6, WAM 36–84; stn 022, 1, WAM 32–84; stn 023, 2, WAM 30–84; stn 090, 1, WAM 33–84.

Remarks

Flabellum hoffmeisteri is most similar to *F. tuthilli*, but can be distinguished by having lower calicular apices; a more elongate corallum with ridged primary costae that reach almost to the calicular edge; striped costae; and less septa at an equivalent

GCD, a full fourth cycle of 128 septa occurring only in the very largest (GCD = 60 mm) *F. hoffmeisteri* but already present in medium-sized coralla (GCD 36 mm) of *F. tuthilli*. Also, although found at the same depth range, the two species overlap in distribution only off western Tasmania, most of the records of *F. tuthilli* being from the Great Australian Bight, where *F. hoffmeisteri* has not been collected.

Distribution

Western Australia: continental slope of northwestern coast from Cartier Island to Port Hedland; 302–544 m; soft (muddy) substrates. Elsewhere: Indonesia; Kermadec and Colville Ridges; off Victoria and Tasmania; 110–646 m (Cairns and Zibrowius 1997).

Flabellum (U.) *tuthilli* Hoffmeister, 1933

Flabellum tuthilli Hoffmeister, 1933: 7–8, pl. 1, figs. 3–5.—Cairns and Parker, 1992: 46–47, pl. 16, figs. a–c (synonymy and description).

New Record

Saxon Progress: stn RP–8, 1, NMV F78389.

Remarks

The specimen reported above is the largest known, measuring 50.5 × 37.6 mm in calicular diameter and 33.9 mm in height, and having 128 septa.

Distribution

Western Australia: continental slope of southern coast (Great Australia Bight from Bremer Bay to South Australia); 347–550 m. Elsewhere: Great Australia Bight off South Australia to western Tasmania; 348–824 m (Cairns and Parker 1992).

Flabellum (U.) *marenzelleri* Cairns, 1989

Flabellum marenzelleri Cairns, 1989: 57–58, pl. 30, figs. a–e (synonymy and description).—Cairns and Zibrowius, 1997: 156.

New Records

Soela: stn 01/84/54, 1, USNM 96639; stn 01/84/55, 1, WAM 557–84; stn 01/84/87, 1, WAM 684–84.

Lady: stn RW96–18, 12: 10 (NTM C8080), 2 (USNM 98512).

Distribution

Western Australia: continental slope of northwestern coast south of Cartier Island and off Dampier Land; 260–348 m. Elsewhere: Philippines and Indonesia; 240–390 m (Cairns and Zibrowius 1997).

Flabellum (U.) *deludens* Marenzeller, 1904

Flabellum deludens Marenzeller, 1904: 269–272, pl. 17, figs. 10, 10a.—Cairns, 1989: 55–56, pl. 29, figs. a–f (synonymy and description); 1994: 73, pl. 32, figs. d–e.—Cairns and Zibrowius, 1997: 154–156.

New Records

Soela: 02/82/10B, 1, WAM 99–83; stn 01/84/67, 1, WAM 441–96.

Distribution

Western Australia: continental slope of northeastern coast from Scott Reef to Port Hedland; 348–360 m. Elsewhere: Indo-West Pacific (northern Indian Ocean through Indonesia to Japan); 106–1035 m (Cairns and Zibrowius, 1997).

Genus *Truncatoflabellum* Cairns, 1989

Truncatoflabellum angiosomum (Folkesson, 1919) comb. nov.

Figures 7a–c, 8a

Flabellum angiosomum Folkesson, 1919: 5, pl. 1, figs. 1–3.—Not Cairns, 1995: 99, pl. 32, figs. d–f (=new species, Cairns, in press).

Truncatoflabellum spheniscus – Cairns and Zibrowius, 1997: 165–166 (in part: figs. 23 a–b; KH72–1–29 and 30).

New Records

Soela: stn 02/82/54A, 1, WAM 36–83; stn 04B/82/71, 1, WAM 344–89; stn 05/82/13, 3: 2 (WAM 51–83), 1 (USNM 96640); stn 05/82/61, 1, WAM 76–83; stn 05/82/63, 1, WAM 78–83.

Dorothea: 64 km W Cape Jaubert, 40 m, 13 X 1962, 4: 2 (WAM 254–93), 2 (USNM 96643); 57 km SW Adele Island, 73 m, 17 X 1962, 3, WAM 255–93; 208 km ENE Troughton Island, 91 m, 23 X 1962, 1, WAM 256–93.

Kunmuniyah: stn BG13, 2, NTM C8000; stn BG27, 3, NTM C8044; stn BG28, 3, NTM C8045; stn BG39, 1, NTM C8048; stn BG83, 2, NTM C8026.

Lady Basten: stn LB3(t), 1, WAM 10–96.

Lady: stn RW96–5, 7, NTM C8063.

Other records: Middle Pass, Darwin, 20 m, 28 XI 1994, 1, NTM C12333.

Description

Angle of curved, rounded thecal edges 105°–200°, but usually about 180°; angle of thecal faces 15°–25°. Holotype 45.2 × 14.7 mm in calicular diameter and 34.2 mm in height, with a basal scar 4.3 × 3.3 mm in diameter; however, largest known specimen (NTM C12333) 63.3 × 19.9 mm in calicular diameter and 42.1 mm in height. Upper calice strongly arched in a semi-circle; GCD:LCD =

3.0–3.2. Basal scar small and elliptical: 2.8–4.3 x 2.5–3.3 mm in diameter. One pair of short, downward projecting thecal edge spines occurs within 2–3 mm of basal scar. Edge spines usually only apparent on small specimens, those of larger coralla often breaking off and their stubs covered by encrusting organisms. Thecal faces usually highly encrusted with calcareous epifauna, including: bivalves, serpulids, barnacles, bryozoa, foraminifera, and acrothoracican cirripede borings. Theca otherwise white. Septa hexamerally arranged in 6 and often a partial 7th cycle in larger coralla according to the formula: S1–4>>S5>S6>S7. S7 begin to appear at a GCD of 30–33 mm; the holotype (GCD = 45.2) has a complement of 50:50:100:68 (268 septa); and larger coralla increase the number of equally large primary septa to 66. The shape of the primary septa (S1–4) is complex. Within 0.3–0.4 mm of the calicular edge these septa are notched, below which they broaden into a wide lobe that often rises slightly above the calicular edge. Midway to columella the axial edge of an S1–4 is slightly concave, but nearer the columella the septum widens. Inner edges of S1–4 straight and thin except near the columella, where they thicken. S5 only about 1/3 width of S1–4 near the calicular edge, but about 4/5 width of S1–4 lower in fossa. S6 about half width of S5. S7 same width as S6 but do not extend as far downward from calicular edge. Fossa deep and elongate, containing a trabecular columella about 1.5 mm wide.

Remarks

Because of my previous confusion in identifying this species, a complete description is provided above, based on the holotype and additional specimens from the same region. Comparisons to *T. spheniscus* are made in the account of that species and in Table 4.

Although not apparent from the original description, the base of the holotype bears a natural scar resulting from transverse division, and the remnants of two thecal edge spines, which clearly places this species in *Truncatoflabellum*.

Distribution

Western Australia: continental shelf of northwestern coast from Joseph Bonaparte Gulf to Nickol Bay; 22–136 m; 23.9° to 28.8°C; sandy, shelly substrates. Elsewhere: Northern Territory (Beagle Gulf and Anson Bay); 15–115 m; sand and gravel substrates.

Truncatoflabellum formosum Cairns, 1989

Truncatoflabellum formosum Cairns, 1989: 69–70; 1994: 77, pl. 33, figs. g–h.—Cairns and Zibrowius, 1997: 169–170.

New Records

Lady Basten: stn LB5(s), 8, exWAM 24–96; stn LB6(s), 1, WAM 44–96.

Remarks

Among the Western Australian *Truncatoflabellum*, *T. formosum* is most similar to *T. australiensis*, but can be distinguished (Table 4) by having a slightly smaller basal scar, and decamerally arranged septa, which results in 80, instead of 96 septa.

Most (7 of 9) of the specimens reported above bear up to seven thecal burrows of acrothoracican cirripedes.

Distribution

Western Australia: continental shelf of northwestern coast southwest of Rowley Shoals; 160–173 m. Elsewhere: ?Indian Ocean; western Pacific from Japan through Indonesia; 42–933 m (Cairns and Zibrowius 1997).

Truncatoflabellum australiensis sp. nov.

Figures 7 d–f, 8 b

Records

Other records: “between Shark Bay and Onslow”, depth unknown, coll. W. and W. Poole, 1966, holotype, WAM 169–83, and 5 paratypes, WAM 171– and 172–83 and 442–96.

Soela: stn 05/82/37, 2 paratypes, WAM 59–83; stn 05/82/42, 1 paratype, WAM 61–83; stn 05/82/47, 2, WAM 63– and 66–83.

Umataka Maru: stn 6927, 2 paratypes, WAM 102–84.

Sprightly: stn 34M, 1 paratype, WAM 134–83.

Diamantina: stn 208, 2 paratypes, WAM 224– and 225–93.

Lady Basten stn: LB5(s), 19 paratypes, WAM 24–96.

W.A. Hawaiian Expedition: 16–32 km NNW Anchor Island, 119 m, 17 VI 1960, 9 paratypes: 6 (WAM 144–83, 231– and 259–93), 3 (USNM 96652).

Lady: stn RW96–17, 1 paratype, NTM C8070.

Type Locality

“Between Shark Bay and Onslow, WA”; depth unknown.

Description

Anthocyathus: Angle of thecal edges 44°–73°; angle of thecal faces 18°–28°. Holotype 21.9 x 10.8 mm in calicular diameter and 17.9 mm in height, with a basal scar 7.1 x 3.5 mm in diameter; largest specimen 25 mm in GCD. Upper calicular edge only slightly arched: GCD:LCD = 1.95–2.35. Basal scar elliptical and of moderate size, its greater diameter ranging from 5.5 to 8.6 mm. Two or 3

Table 4 Characteristics of the Anthocyathi of the eight Western Australian Species of *Truncatoflabellum* (arranged from smallest to largest basal scar diameter).

	Greater Diameter Basal Scar (mm)	Septal Symmetry and Number	Edge Angle	Inner Edges of Larger Septa	GCD:LCD	Pairs of Edge Spines	Thecal Colour	Other Characters
<i>T. angiospermum</i>	2.8-4.3	S1-4>>S5>S6>S7 (-268 septa)	105°-180°-200°	Straight	3.0-3.2	1	White	Thecal edges usu. curved; edge spines often broken; calicular edge highly arched
<i>T. formosum</i>	4.2-5.5	20:20:40 (80 septa) common	57°-66°	Sinuuous	1.8-2.1	2-3	Brown-striped	Smooth calicular edge; acrothoracican cirripede parasites
<i>T. australiensis</i>	5.5-8.6	S1-3>S4>S5 (96 septa)	44°-73°	Sinuuous	1.9-2.4	2-3	Brown-striped	Calicular edge slightly scalloped
<i>T. paripavoninum</i>	6.8-14.5	S1-3>S4>S5>S6 (192 septa)	57°-138°	Straight to sl. sinuous	1.4-2.0	None	White or brown	Thecal edges acute; deep-water: over 350 m; corallum fragile
<i>T. spheniscus</i>	10-12	40-44:40-44:80-88:4-14 (-190 septa)	82°-86°	Straight, thickened	2.8-3.6	1	White	
<i>T. aculeatum</i>	10.7-15.2	S1-3>S4>S5 (96) to 25-40:25-40:50-80 (160 septa)	31°-82°	Sinuuous (fine)	1.8-3.7	usu. 1	Milky white	
<i>T. veroni</i>	14.4-15.8-18.3	S1-4>S5>S6>S7 (192-212 septa)	94°-127°	Sinuuous (fine)	3.0-3.2	1	White	
<i>T. macroschura</i>	19.7-24.4-30.4	S1-4>>S5>S6>S7 (192 septa)	55°-87°	Sinuuous	2.5-3.1	1	White	Columella wide: 2.5-3.5 mm

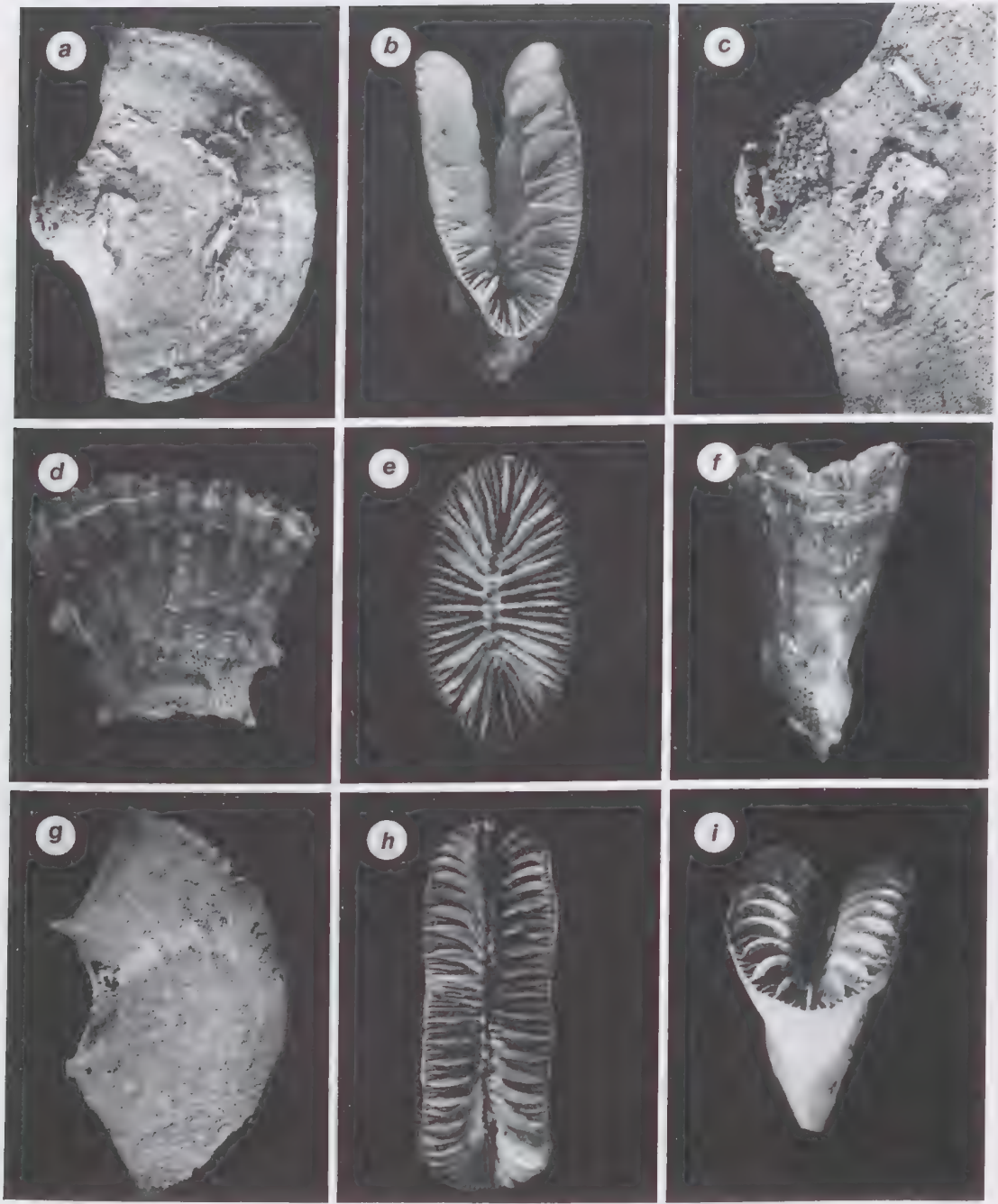


Figure 7 a-c, *Truncatoflabellum angiosomum*, holotype, SMNH 4752: a-b, side and edge views, x 1.5, x 1.7, respectively; c, basal scar, x 4.8. d-f, *T. australiensis*: side, calicular, and edge views of holotype, x 2.4, x 2.4, x 2.8, respectively. g-i, *T. veroni*: side, calicular, and edge views of holotype, x 1.2, x 1.1, x 1.6, respectively.

pairs of thin thecal edge spines present, occasionally a different number on opposite edges of the same corallum. Theca only lightly encrusted with calcareous epifauna; however, one corallum (*Soela* stn 05/82/42) is heavily infested with acrothoracican cirripede borings. Theca light brown, more intensely pigmented along the S1–2 as radiating stripes. Septa hexamerally arranged in 5 cycles (S1–3>S4>S5, 96 septa), the fifth cycle complete at a GCD as small as 12 mm. S1–3 slightly exsert, having sinuous axial edges; in some specimens S3 are narrower than S1–2. S4 about 3/4 width of the S1–3; S5 quite small, only 1/5 width of the S4. Fossa deep and narrow, containing a trabecular columella about 1.3 mm wide.

Anthocaulus: Only two specimens of the attached anthocaulus stage are known (WAM 259–93, WAM 442–96, Fig 8b), both of which are still firmly attached to a short anthocyathus stage at a height of 8.8–8.9 mm. A fine, white, crescent-shaped line on the theca indicates the eventual line of transverse division, which is also indicated inside the corallum by an incipient endothecal dissepiment. Pedicel of anthocauli 1.5–1.6 mm in diameter; a pair of elongate, (up to 5 mm) hollow thecal edge spines also occurs on the anthocaulus.

Remarks

Among the approximately 28 extant species within the genus, only three others have predominantly hexameral septal symmetry arranged in 5 cycles: *T. candeanum* Milne Edwards and Haime, 1848a; *T. carinatum* Cairns, 1989; and *T. incrustatum* Cairns, 1989 (see Cairns 1989: Table 6). *T. australiensis* is most similar to *T. candeanum*, particularly in shape, size, pigmentation, and spination, but differs in having a larger scar diameter, a non-scalloped calicular edge, and a lower face angle, which results in a larger GCD:LCD (1.95–2.35 vs 1.6–1.7 for *T. candeanum*). Furthermore, although *T. candeanum* can have 5 full cycles of septa, this number is usually not attained until a GCD of about 24 mm, whereas 96 septa are present in *T. australiensis* at the relatively small GCD of 12 mm. *T. australiensis* is relatively easily distinguished from other Western Australian *Truncatoflabellum* by having 2 or 3 pairs of thecal edge spines, brown-striped theca, and only 96 septa (Table 4).

Distribution

Western Australia: continental shelf of western coast south of Cartier Island to Houtman Abrolhos Islands; 90–180 m.

Etymology

This species is named for the continent from which it was described.

Truncatoflabellum paripavoninum (Alcock, 1894)

Flabellum pari-pavoninum Alcock, 1894: 187.

Truncatoflabellum paripavoninum – Cairns, 1989: 72–73, pl. 37, figs. j–l, pl. 38, fig. a (synonymy and description); 1995: 113–114, pl. 37, figs. d–e.—Cairns and Zibrowius, 1997: 169, fig. 22 f.

New Records

Soela: stn 01/84/60, 1, WAM 577–84; stn 01/84/77, 2: 1 (WAM 529–84), 1 (USNM 96650); stn 01/84/120, 2, WAM 699– and 702–84.

Distribution

Western Australia: continental slope of northwestern coast from north of Browse Island to south of Rowley Shoals; 394–530 m; soft substrates. Elsewhere: Indo-West Pacific from Laccadive Sea through Indonesia and Philippines and Kermadec Islands; 411–1450 m (Cairns and Zibrowius 1997).

Truncatoflabellum spheniscus (Dana, 1846)

Euphyllia spheniscus Dana, 1846: 160–161, pl. 6, figs. 1a–c.

Flabellum rubrum – Folkeson, 1919: 4–5 (in part: specimen #1).

Truncatoflabellum spheniscus – Cairns, 1989: 65–66, pl. 32, figs. g–k; 1994: 76, pl. 33, figs. a–d.—Cairns and Zibrowius, 1997: 165–166 (in part: those specimens with large basal scars).

New Records

Soela: stn 01/69, 1, WAM 371–80.

Lady: stn RW96–5, 2, NTM C8062.

Remarks

Although similar to *T. angiosomum*, particularly in septal shape and face angle, *T. spheniscus* can be distinguished from that species by its larger basal scar (10–12 mm in greater diameter), lesser edge angle (80°–90°), and smaller size with consequently fewer septa (see Table 4).

Distribution

Western Australia: continental shelf of northwestern coast (Joseph Bonaparte Gulf, Cape Jaubert and Long Island, Passage Islands); 16–32 m. Elsewhere: western Pacific from Japan through Indonesia; Gulf of Carpenteria; Torres Strait; 2–174 m (Cairns and Zibrowius 1997).

Truncatoflabellum aculeatum (Milne Edwards and Haime, 1848a)

Flabellum aculeatum Milne Edwards and Haime, 1848a: 272, pl. 8, figs. 3, 3a.

Flabellum rubrum – Folkesson, 1919: 4–5 (in part: specimens 2, 3, 5).

Truncatoflabellum aculeatum – Cairns, 1989: 61, 64, pl. 31, figs. h–l, pl. 32, figs. a–c (synonymy and description).—Cairns and Zibrowius, 1997: 166–167.

New Records

Soela: stn 04B/82/76A, 1, WAM 42–84; stn 05/82/27, 1, WAM 54–83.

Dorothea: 208 km ENE Troughton Island, 91 m, 23 X 1962, 1, WAM 257–93.

Kunmuniyah.: stn BG13, 3, NTM C8002.

Other records: Suomi Island, Easter Group, Abrolhos Islands, 42 m, 22 VIII 1977, 1, WAM 264–93; Roebuck Bay, Broome, 9–15 m, coll. A. A. Livingston, 1929, 3, AMS G13343.

Distribution

Western Australia: continental shelf of western coast from Cape Jaubert to Abrolhos Islands, and west of Beagle Gulf; 11–115 m. Elsewhere: western Pacific from Philippines through Indonesia to Northern Territory (Beagle Gulf and Anson Bay); 11–91 m (Cairns and Zibrowius 1997).

Truncatoflabellum veroni sp. nov.

Figures 7 g–i, 8 c

Records

Soela: stn 02/82/54A, holotype and 16 paratypes: 12 (WAM 89–83 and 91–83), 4 (USNM 96655); stn 04B/82/51A, 1 paratype, WAM 624–88; stn 05/82/12, 2 paratypes: 1 (WAM 49–83), 1 (USNM 96658); stn 05/82/unknown station between Dampier and Port Hedland, 2 paratypes, WAM 47– and 48–83.

Dorothea: 64 km W of Cape Jaubert, 40 m, 13 X 1962, 1 paratype, WAM 443–96; 208 km ENE Troughton Island, 91 m, 23 X 1962, 1 paratype, USNM 96660.

WA Hawaiian Expedition: 22 km NNW Anchor Island, Onslow, 119 m, 17 VI 1960, 1 paratype, WAM 445–96.

Kunmuniyah.: stn BG13, 1 paratype, NTM C8001; stn BG20, 6 paratypes, NTM C8042; stn BG21, 3 paratypes, NTM C8004; stn BG28, 1 paratype, NTM C8008; stn BG36, 1 paratype, NTM C8047; stn BG91, 1 paratypes, NTM C8031; stn BG101, 2 paratypes, NTM C8054.

Lady Basten: stn LB1b(s), 2 paratypes, WAM 6–96.

Other records: Middle Pass, Darwin, 20 m, 28 XII 1994, 1 paratype, NTM C12333; Gunn Point, Shoal Bay, Darwin, 1 paratype, NTM C7994.

Type Locality

19°59'S, 117°16'E (off Port Walcott, WA); 50–52 m.

Description

Anthocyathus: Angle of straight, rounded thecal edges 94°–127°; angle of thecal faces 23°–32°. Largest specimen (the holotype) 56.5 x 17.6 mm in calicular diameter and 26.9 mm in height, with a basal scar diameter of 17.7 x 6.5 mm. Calicular edge and basal scar strongly arched, both roughly concentric to the point of attachment of anthocaulus; GCD:LCD = 3.0–3.2. Basal scar ranges from 14.4 to 18.3 mm in greater diameter (ave. = 15.85, N = 14). One pair of downward curving thecal edge spines occurs directly adjacent to basal scar; thecal spines up to 7 mm in length but usually broken or worn in larger coralla. Theca often encrusted with calcareous epifauna, including bryozoa, serpulids, and foraminifera; otherwise corallum uniformly white. Septa hexamerally arranged in 6 cycles (S1–4>>S5>S6, =192 septa), the sixth cycle complete at a GCD as low as 36 mm. Larger coralla (>50 mm GCD) often have additional primary septa (e.g., 50 equally large septa instead of 48, and some pairs of S7), the holotype having a total of 212 septa. S1–4 shaped as in *T. spheniscus* and *T. angiosomum*: notched near the calicular edge, slightly exsert, slightly constricted midway to columella, and broader near columella. Axial edges of S1–4 finely sinuous. S5 quite narrow at calicular edge, but widen to 2/3 width of S1–4 lower in fossa. S6 rudimentary. Fossa deep and elongate, containing a well-developed trabecular columella about 1.5 mm in width.

Anthocaulus 10–12 mm in height and 1.7–2.0 mm in pedicel diameter, having 1 pair of elongate thecal edge spines.

Remarks

Truncatoflabellum veroni is similar to *T. aculeatum* (see Table 4), but can be distinguished by having a larger basal scar size, a higher edge angle (usually over 90° vs less than 90°), and more septa. Except for *T. macroeschara*, it has a largest basal scar diameter of any species in the genus.

Distribution

Western Australia: continental shelf of northwestern coast from Cape Jaubert to Onslow; 40–119 m; sandy substrates. Elsewhere: Northern Territory (Anson Bay and Beagle Gulf); 15–31 m; coarse sand and gravel substrates.

Etymology

This species is named in honour of J. E. N. "Charlie" Veron, who has done much to advance our knowledge of Australian reef corals and who published several first records of azooxanthellate corals from Australia (Veron 1986).

Truncatoflabellum macroeschara sp. nov.

Figure 8 d–e, g–i

?*Flabellum* sp. Veron, 1986: 603, black and white illustration.

Records

Soela: stn 05/82/13, holotype and 1 paratype, WAM 50–83; stn 02/82/9, 1 paratype, WAM 97–83; stn 02/83/13A, 2 paratypes, WAM 77– and 98–84; stn 04B/82/64, 1 paratype, WAM 82–83; stn 05/82/60, 1 paratype, WAM 75–83; stn 05/82/65, 1 paratype, WAM 79–83.

Hai Kung: stn MFG81, 1 paratype, NMV F78390.

WA Hawaiian Expedition: 16–22 km NNW Anchor Island, Onslow, 119 m, 17 VI 1960, 2 paratypes: 1 (WAM 230–93), 1 (USNM 96661).

Lady Basten: stn LB4(s), 1 paratype, WAM 13–96; stn LB5(s), 1 paratype, WAM 34–96; stn LB5(t), 3 paratypes, WAM 17–96; stn LB6(t), 3 paratypes: 2 (WAM 37– and 39–96), 1 (USNM 96664).

Lady: stn RW96–14, 1 paratype, NTM C8068.

Type Locality

19°52.3'S, 117°16.1'E (east of Glomar Shoal, WA); 56–58 m.

Description

Angle of straight, rounded thecal edges 55°–87°; angle of thecal faces 22°–27°. Holotype 46.2 × 15.8 mm in calicular diameter and 22.5 mm in height, with a basal scar diameter of 25.1 × 10.1 mm; however largest specimen (WAM 39–96) 106.7 mm in GCD. Calicular edge and basal scar moderately arched; GCD:LCD = 2.5–3.1. Basal scar enormous, ranging from 19.7 to 30.4 mm in greater length and 10–12 mm in width (ave. length = 24.37 mm, N = 8). One pair of downward curving thecal edge spines occurs adjacent to basal scar. Theca often encrusted with foraminifera, serpulid tubes, bryozoans, gastropod egg cases, gastropods (limpets), and bivalves (oysters); otherwise corallum white. Septa hexamerally arranged in 6 cycles (S1–4>>S5>S6, =192 septa); however, larger coralla have additional pairs of S7 but never a full cycle. S1–4 shaped as in *T. veroni* and several other species; axial edges straight in upper fossa, but moderately sinuous adjacent to columella. S5 narrow at calicular edge but about half width of S1–4 lower in fossa. S6 rudimentary. Fossa deep and wide, containing a well-developed trabecular columella 2.5–3.5 mm in width.

Only one anthocaulus is known (WAM 230–93, Fig 8d), measuring 23.5 × 10.9 mm in calicular diameter, 15.9 mm in height, and having a pedicel 2.0 mm in diameter and a pair of thecal edge spines 7 mm long. It appears to be a mature anthocaulus, perhaps just having budded an anthocyathus.

Remarks

Truncatoflabellum macroeschara differs from all other species in the genus by having such a large basal scar and a very wide columella. Among Australian species, it is most similar to *T. veroni*. In addition to its larger basal scar and columella, *T. macroeschara* can be distinguished from *T. veroni* by its smaller edge angle (less than 90° vs more than 90°) and smaller GCD:LCD (see Table 4).

Veron's (1986: 603) illustration of a *Truncatoflabellum* implies a greater basal scar diameter of 33–34 mm, which is unlikely. The stated magnification of the figure is probably too low, and these specimens are probably either *T. macroeschara* or *T. veroni*.

Distribution

Western Australia: continental shelf of northwestern coast from Sahul Bank (Holothuria Reef) to Onslow; 58–201 m; 19°–24.1°C; sandy and rubble substrates.

Etymology

The species name *macroeschara* (Greek *makros*, long + *eschara*, scar) alludes to the extremely long basal scar of the anthocyathus.

Genus *Placotrochus* Milne Edwards and Haime, 1848a*Placotrochus laevis* Milne Edwards and Haime, 1848a

Figure 8 f

Placotrochus laevis Milne Edwards and Haime, 1848a: 283, pl. 8, figs. 15, 15a.—Semper, 1872, 251–252, pl. 18, figs. 11–13.—Folkesson, 1919: 5–6.—Cairns, 1989: 75–76, pl. 39, figs. c–g (synonymy and description).—Cairns and Zibrowius, 1997: 175.

Placotrochus sp. Veron, 1986: 603, black and white fig.

New Records

Soela: stn 02/82/12A, 1, WAM 100–83; stn 02/82/54A, 9: 6 (WAM 19–88 and 447–96), 3 (USNM 96677).

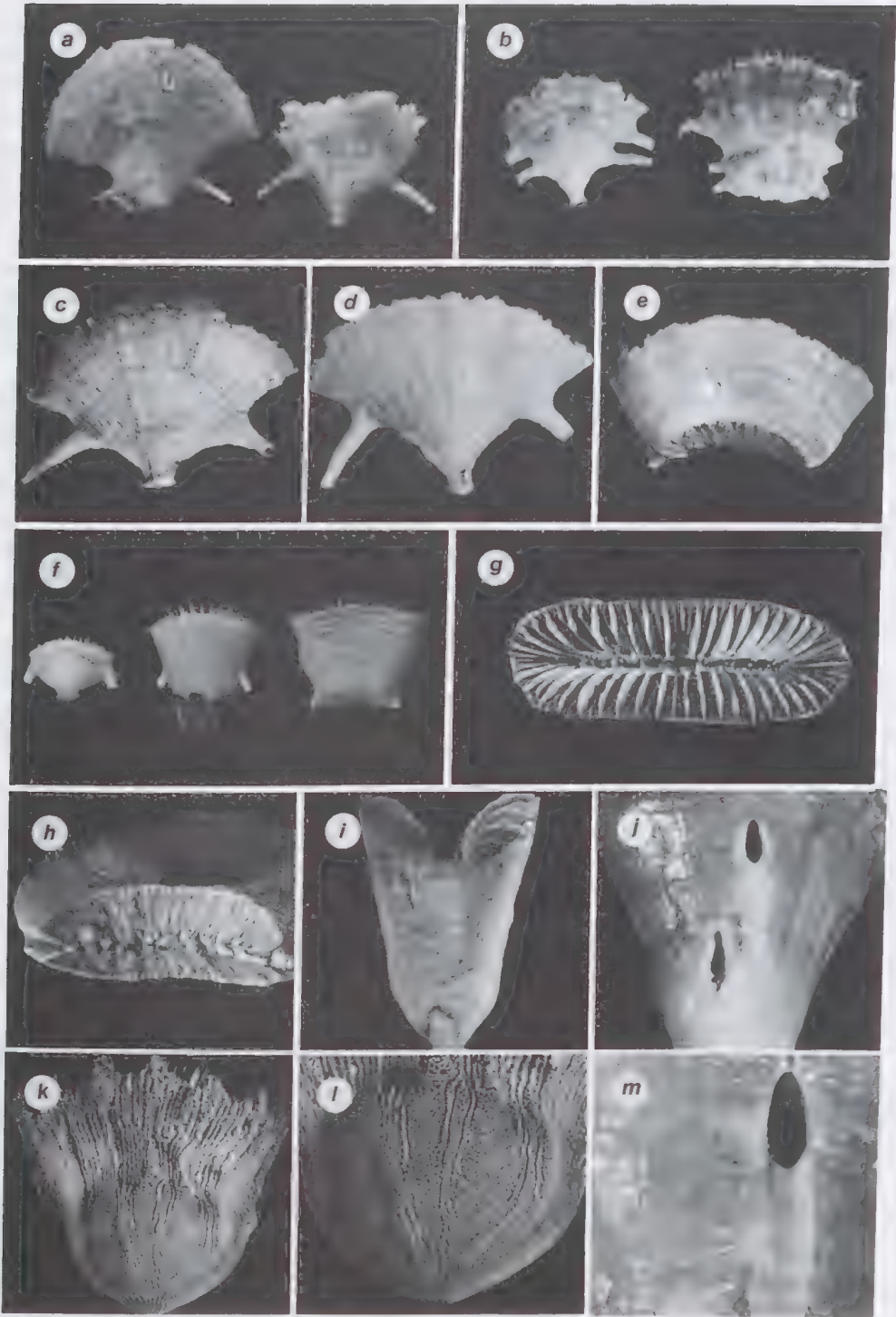
Sprightly: stn SP04/12/41, 1, WAM 227–92.

Umataka Maru: stn 6927, 2, WAM 99–84 and 219–92.

Moresby: stn 12, 1, WAM 226–92; stn 14, 1, WAM 2–83.

Lady Basten: stn LB1b(s), 1, WAM 7–96.

Kunmumyah: stn BG2, 1, NTM C7999; stn BG13, 20, NTM C8046; stn BG20, 6, NTM C8003; stn BG21, 3, NTM C8043; stn BG26, 2, NTM C8005; stn BG27, 4, NTM C8007; stn BG28, 5, NTM C8009; stn BG36, 1, NTM C8010; stn BG39, 2, NTM C8011; stn



BG46, 2, NTM C8012; stn BG47, 2, NTM C8049; stn BG56, 2, NTM C8016; stn BG77, 53, NTM C8019; stn BG80, 3, NTM C8021; stn BG82, 70, NTM C8052; stn BG83, 2, NTM C8023; stn BG86, 3, NTM C8029.

Other records: Stn pAe, Mermaid Sound, Dampier Archipelago, 9 m, 10 II 1981, 1, WAM 341-88; stn Pac, *Ibid.*, 7-9 m, 13 II 1981, 1, USNM 96668.

Distribution

Western Australia: continental shelf of northwestern coast from Bonaparte Gulf to Dampier Archipelago; 9-90 m. Elsewhere: Indo-West Pacific from Gulf of Manaar through Indonesia and the Philippines; Northern Territory (Beagle Gulf and Anson Bay); Queensland; 6-289 m (Cairns and Zibrowius 1997).

Genus *Javania* Duncan, 1876

Javania lamprotichum (Moseley, 1880)

Figure 8 j, m

Desmophyllum lamprotichum Moseley, 1880: 41-42, figs. 1-2.

Javania lamprotichum - Cairns, 1995: 112, pl. 37, figs. b-c (synonymy and description).—Cairns and Zibrowius, 1997: 164.

New Records

Soela: stn 02/82/14, 1, WAM 101-83; stn 02/82/16, 4: 3 (WAM 103- and 104-83), 1 (USNM 96678).

Lady Basten: stn LB7(s), 2: 1 (WAM 47-96), 1 (USNM 96682).

Remarks

One specimen from *Lady Basten* station LB7(s) was infested with several large acrothoracican cirripedes (Figure 8 j, m), the elongate thecal efferent pores up to 3.6 mm in length and 1.8 mm in width. This parasitism was previously reported by Cairns and Zibrowius (1997).

Distribution

Western Australia: northwestern coast from south of Rowley Shoals to Port Hedland; 200-201 m. Elsewhere: central and western Pacific (Hawaiian Islands; Johnston Atoll; Philippines;

Kermadec Ridge); 191-842 m (Cairns and Zibrowius 1997).

Genus *Rhizotrochus* Milne Edwards and Haime, 1848a

Rhizotrochus tuberculatus (Tenison Woods, 1879)

Vasillum tuberculatus Tenison Woods, 1879: 93, pl. 10, figs. 3a, b.

Monomyces radiatus - Squires, 1966: 172, pl. 1, figs. 1-2.—Shepherd and Veron, 1982: 177, fig. 4.54f.

Monomyces - Veron, 1986: 603.

Rhizotrochus tuberculatus - Cairns and Parker, 1992: 49-50, figs. 16 g-i (synonymy and description).—Johnson, Baarli, and Scott, 1995: 95, fig. 9A-C.

New Records

Beacon Island, Wallabi Group, Abrolhos Islands, depth unknown, 24 IV 1974, 1, WAM 247-93; Salmon Point, Rottnest Island, depth unknown, 1950, 1, WAM 127-58; *Ibid.*, 1-2 m, 17 I 1991, 2: 1 (WAM 9-91), 1 (USNM 96683); Cowaramup Bay, depth unknown, 24 II 1985, 1, WAM 57-85; Cowaramup Bay, depth unknown, 21 X 1989, 1, WAM 1131-89; Ellenbrook, west of Margaret River, 1 III 1976, 1, WAM 249-93; *Ibid.*, 31 VIII 1976, 4, WAM 251-93.

Distribution

Western Australia: continental shelf of southwestern coast from Abrolhos Islands to Hopetoun, including Late Pleistocene of Cape Burney, near Geraldton; 1-2 m. Elsewhere: South Australia, Victoria, and Tasmania; 0-73 m (Cairns and Parker 1992).

Genus *Polomyces* Cairns, 1979

Polomyces wellsi Cairns, 1991

Polomyces wellsi Cairns, 1991: 22, pl. 8, figs. f, i, pl. 9, figs a-b; 1995: 108-109, pl. 35, figs. d-f, map 10.—Cairns and Zibrowius, 1997: 160-161.

New Record

Lady: stn RW96-29, 1, NTM C8089.

◀ **Figure 8** a, *Truncatoflabellum angiosomum*, WAM 255-93, a young anthocyathus (left) and an anthocaulus (right), x 1.7. b, *T. australiensis*, paratypes, WAM 442-96, anthocaulus (left) and small anthocyathus (right), x 1.7. c, *T. veroni*, paratype, WAM 445-96, anthocaulus, x 2.3; d-e, g-i, *T. macroeschara*: d, paratype, WAM 230-93, anthocaulus, x 2.0; e, g-i, side, calicular, basal scar, and edge views of holotype, x 1.0, x 1.2, x 1.7, x 1.9, respectively. f, *Placotrochus laevis*: NTM TP32, series showing an anthocaulus with incipient fracture line, an anthocyathus still attached to anthocaulus, and a detached anthocyathus, x 2.0. j, m, *Javania lamprotichum*, *Lady Basten* stn LB7(s), USNM 96682, acrothoracican cirripede borings, x 2.4, x 13, respectively. k-l, *Endopachys bulbosa*, *Soela* stn 01/84/85, WAM 678-84, side view and enlargement of massive base, x 1.2, x 1.8, respectively.

Distribution

Western Australia: continental slope of northwestern region between Browse and Cartier Islands; 400–420 m. Elsewhere: Philippines to New Zealand; Galápagos; 355–1165 m (Cairns and Zibrowius 1997).

Genus *Gardinieria* Vaughan, 1907

Gardinieria hawaiiensis Vaughan, 1907

Gardinieria hawaiiensis Vaughan, 1907: 65–66, pl. 4, fig. 1.—Cairns, 1995: 110–111, pl. 36, figs. c–f, i (synonymy and description).

New Records

Soela: stn 01/84/82, 1, WAM 676–84; stn 01/84/82A, 1, WAM 749–84.

Distribution

Western Australia: continental slope of northwestern coast from Cartier Island to south of Scott Reef; 304–400 m. Elsewhere: central and western Pacific (Hawaiian Islands; Philippines; New Zealand region); 142–602 m (Cairns 1995).

Gardinieria philippinensis Cairns, 1989

Gardinieria philippinensis Cairns, 1989: 82, pl. 42, fig. a.—Cairns and Zibrowius, 1997: 162–163.

? *Gardinieria* Veron, 1986: 603.

New Record

Soela: stn 01/84/85, 1, WAM 680–84.

Distribution

Western Australia: south of Scott Reef; 220–224 m. Elsewhere: Philippines; Indonesia; 192–494 m (Cairns and Zibrowius 1997).

Suborder Dendrophylliina

Family Dendrophylliidae Gray, 1847

Genus *Balanophyllia* Searles Wood, 1844

Balanophyllia carinata (Semper, 1872)

Rhodopsammia carinata Semper, 1872: 257, pl. 19, figs. 6a–b.

Balanophyllia carinata: Zibrowius, 1985: 235–238, figs. 15–24 (synonymy and description).—Cairns and Zibrowius, 1997: 175–176.

New Records

Lady Basten: stn LB4(s), 10: 8 (WAM 11–96), 2 (USNM 96688).

Distribution

Western Australia: known only from the

continental shelf off Port Hedland; 112–124 m. Elsewhere: tropical Indo-West Pacific from Somalia to Chesterfield Islands; 33–100 m (Cairns and Zibrowius 1997).

Balanophyllia imperialis Kent, 1871

Balanophyllia imperialis Kent, 1871: 284, pl. 23, figs. 5a–b.—Cairns and Zibrowius, 1997: 184–185, figs. 26 c–f (synonymy and description).

New Record

Lady Basten: stn LB5(s), 1, WAM 36–96.

Lady: stn RW96–8, 1, NTM C8067.

Distribution

Western Australia: Joseph Bonaparte Gulf and Port Hedland; 100–150 m. Elsewhere: western Pacific from South China Sea through Indonesia; 18–170 m (Cairns and Zibrowius 1997).

Balanophyllia gigas Moseley, 1881

Balanophyllia gigas Moseley, 1881: 193.—Cairns, 1994: 83, pl. 35, figs. j–l (synonymy and description); 1995: 119–120, pl. 40, figs. f–h.—Cairns and Zibrowius, 1997: 182.

New Records

Soela: stn 01/84/55, 5: 4 (WAM 562–84), 1 (USNM 96689); stn 01/84/56, 3, WAM 567–84; stn 01/84/57, 1, WAM 736–84; stn 01/84/87, 1, WAM 686–84.

Distribution

Western Australia: continental slope of northwestern coast off Cape Leveque, Dampier Land; 260–352 m. Elsewhere: Japan; Hawaiian Islands; Philippines; Indonesia; New Zealand; 90–640 m (Cairns and Zibrowius 1997).

Balanophyllia cornu Moseley, 1881

Balanophyllia cornu Moseley, 1881: 192–193, pl. 12, figs. 11–15.—Cairns, 1994: 82–83, pl. 35, figs. f–i (synonymy and description).—Cairns and Zibrowius, 1997: 178–179, figs. 24 d–f.

New Records

Soela: stn 02/82/13A, 7, WAM 79–, 80–, and 92–84; stn 02/82/17, 1, WAM 107–82; stn 01/84/55, 1, WAM 448–96; stn 01/84/56, 1, WAM 35–85; stn 01/84/85, 2: 1 (WAM 449–96), 1 (USNM 96690); stn 01/84/87, 1, WAM 228–92.

Remarks

Of the two growth forms described for this species (Cairns and Zibrowius 1997), the Western Australian specimens are all of the typical form, i.e., having a straight, attached corallum.

Distribution

Western Australia: continental slope of northwestern coast from south of Scott Reef to Port Hedland; 150–404 m; 9.6°–19°C. Elsewhere: Japan through Indonesia; 60–520 m (Cairns and Zibrowius 1997).

***Balanophyllia generatrix* Cairns and Zibrowius, 1997**

Balanophyllia generatrix Cairns and Zibrowius, 1997: 183–184, figs. 25 g–i, figs. 26 a–b.

New Records

Soela: stn 01/84/55, 3 quasicolonies: 2 (WAM 17–85), 1 (USNM 96695); stn 01/84/56, 3 quasicolonies, WAM 564–84; stn 01/84/57, 2 quasicolonies, WAM 16–85; stn 01/84/75, 1 corallum, WAM 798–84; stn 01/84/120, 1 quasicolony, WAM 199–93.

Lady Basten: stn LB7(s), 13 quasicolonies: 11 (WAM 46–96), 2 (USNM 96692).

Distribution

Western Australia: continental slope of northwestern coast from west of Browse Island to south of Rowley Shoals; 200–530 m; soft substrates. Elsewhere: Philippines and Indonesia; 96–535 m (Cairns and Zibrowius 1997).

***Balanophyllia* spp.**

Records

Soela: stn 02/82/9, 1, WAM 96–83; stn 02/82/10A, 10, WAM 46– and 450–96; stn 02/82/13A, 2, WAM 83– and 93–84; stn 05/82/46, 1, WAM 68–83; stn 05/82/47, 1, WAM 64–83; 05/82/59, 1, WAM 704–84.

Sprightly: stn 35M, 1, WAM 362–79.

Diamantina: stn 92, 1, WAM 146–83.

Dorothea: 150 mi (240 km) ENE Troughton Island, 91 m, 1, WAM 258–93.

Other records: Abrolhos Islands, coll. Dakin, 1915, 1, WAM 128–58.

Remarks

The taxonomy of the approximately 54 valid Recent species (Best *et al.* 1995) of *Balanophyllia* is in need of revision. Whereas four species can be identified with some confidence from Western Australia, additional species occur off this coast from the Arafura Sea to Abrolhos (34–201 m), represented by the unidentified specimens listed above. But, until additional specimens are collected from this coast, and the taxonomy of the genus is better known, these specimens will remain unidentified.

Genus *Endopachys* Lonsdale, 1845

***Endopachys grayi* Milne Edwards and Haime, 1848b**

Endopachys grayi Milne Edwards and Haime, 1848b: 82–83, pl. 1, figs. 2, 2a.—Veron, 1986: 610, black and white fig.—Cairns, 1994: 84–85, pl. 36, figs. e, h, pl. 37, fig. i (synonymy and description); 1995: 121–122, pl. 41, figs. c–h (description).—Cairns and Zibrowius, 1997: 185–186.

New Records

Soela: stn 05/82/47, 1, WAM 65–83.

Diamantina: stn 185, 1, WAM 451–96.

Lady Basten: stn LB5(s), 4, WAM 457–96; stn LB5(t), 1, WAM 16–96.

Other records: between Shark Bay and Onslow, no depth, coll. W. and W. Poole, 1966, 1, WAM 168–83.

Remarks

Veron (1986) listed another Recent species of *Endopachys* from Australia: *E. australiae* Tenison Woods, 1878b (type locality: Port Jackson, NSW, 146 m); however, the original description and figure of *E. australiae* are not consistent with a placement in this genus.

Distribution

Western Australia: continental shelf of northwestern coast off Port Hedland and Cape Farquhar; 128–150 m. Elsewhere: Indo-Pacific from southwestern Indian Ocean to Gulf of California, including Japan, New Zealand, and Hawaiian Islands; 37–386 m (Cairns and Zibrowius 1997).

***Endopachys bulbosa* Cairns and Zibrowius, 1997**
Figure 8 k–l

Endopachys bulbosa Cairns and Zibrowius, 1997: 186, figs. 27 a–g.

New Record

Soela: stn 01/84/85, 1, WAM 678–84.

Distribution

Western Australia: off Cape Leveque (south of Scott Reef); 220–224 m. Elsewhere: Arafura Sea south of Tanimbar Islands; 233–251 m (Cairns and Zibrowius, 1997).

Genus *Notophyllia* Dennant, 1899

***Notophyllia piscacauda* sp. nov.**
Figure 9 a–e

Notophyllia sp. Cairns and Parker, 1992: 52 ("sixth undescribed species").

Records

King George Sound, 40–51 m, Verco collection,

holotype and 4 paratypes, SAM H664; King George Sound, 22–26 m, Verco collection, 3 paratypes: 2 (SAM H663), 1 (SEM stub 857, USNM 85715).

Type Locality

King George Sound, W.A.; 40–51 m.

Description

Corallum (anthocyathus) cuneiform, with straight, rounded thecal edges and planar thecal faces. Angle of thecal edges about 33°; angle of thecal faces 10°. Holotype 6.1 × 2.8 mm in calicular diameter and 6.9 mm in height. Upper calicular edge slightly convex; GCD: LCD = 1.9–2.2. Region of basal scar highly compressed laterally and extends into 2 or 3, downward-projecting, triangular wedges: the 2 outer wedges are continuous with the thecal edges, whereas the central wedge is usually smaller (Figure 9d–e). Theca white and only slightly porous, more pores occurring on lower corallum than upper. Theca covered with tall (0.15 mm), circular to elongate (0.1–0.4 mm in length) granules (carinae) oriented longitudinally but not arranged as costae. Intercostal regions 0.05–0.06 mm wide, sometimes trapping irregularly shaped sand grains (Figure 9c). Intercostal regions contain large pores 0.8–1.0 mm in diameter, which penetrate the theca, and much more numerous and smaller (10 µm in diameter) pits. Epithea absent. Anthocaulus unknown.

Septa hexamerally arranged in 4 cycles, pairs of S4 present only in half-systems adjacent to the principal S1, resulting in 32 septa (6:6:12:8). S1 widest and thickest septa, the inner edges of the 4 lateral S1 fusing to the lamellar columella in upper fossa. S2 dimorphic in size, those 4 occurring in the end systems being slightly less wide and thick than the S1, but the 2 S2 occurring in the lateral systems are quite small at the calicular edge, but become wider and fuse to the columella deep within fossa. S3 also dimorphic in size, the 8 in the lateral systems and adjacent half-systems being about the same size as the larger S2, whereas the 4 closest to the principal septa are quite small. The 8 S4, which occur only in the half-systems adjacent to the 2 principal septa, are equal to the smaller S3 in size. Inner edges of all septa straight; septal faces and lamellar columella finely granular.

Remarks

Two Recent and 4 fossil species have been described in the genus *Notophyllia*. Between the 2 Recent species, both of which occur off South Australia (Cairns and Parker 1992), *N. piscacauda* is most similar to *N. etheridgi*, having a similarly shaped highly compressed corallum, but differs in having 32 hexamerally arranged septa (vs 48 decamerally arranged septa), a serrated

anthocyathus base (fishtail shaped), and higher cycle septa that are proportionately much broader than those of *N. etheridgi*. *N. piscacauda* differs from the fossil species in having a more compressed corallum (higher GCD:LCD) and in having a distinctive septal arrangement.

In the course of comparing this new taxon to other species, the types of *N. variolaris* (Tenison Woods, 1878a) were borrowed, a species described from the Balcumbian (Middle Miocene) of Victoria as well as the Recent of New South Wales. Only the 49 Recent syntypes were obtained (AMS G7022), 34 of which are *N. recta* and 15 of which are *N. etheridgi*. The primary description and illustration of *N. variolaris*, however, is based on a single Middle Miocene specimen, which is a valid, and different species from the Recent syntypes. This fossil specimen is herein designated as the lectotype of *N. variolaris*. Among the three fossil species, *N. piscacauda* is most similar to *N. variolaris*, both species having a similar corallum base shape and coarsely granular theca without costae. *N. piscacauda* differs in having a more elongate calice (GCD:LCD = 1.9–2.2 vs 1.4–1.8) and in having hexamerally arranged septa (those of *N. variolaris* being decamerally arranged: 10:10:20).

Distribution

Western Australia: known only from King George Sound; 22–51 m.

Etymology

The species name *piscacauda* (Latin *piscis*, fish + *cauda*, tail) is an allusion to the fishtail-shaped base of the anthocyathus.

Genus *Heteropsammia* Milne Edwards and Haime, 1848b

Heteropsammia cochlea (Spengler, 1781)

Madrepora cochlea Spengler, 1781: 240–248, figs. A–D.

Heteropsammia cochlea – Veron and Pichon, 1980: 416–420, in part: figs. 727, 729 (synonymy and description).—Veron, 1986: 576–577, color figs. 1–2, but not black and white fig. (reversed with figure for *Heterocyathus aequicostatus*, page 559).—Veron and Marsh, 1988: 123.—Hoeksema and Best, 1991: 234–237, figs. 24–28 (synonymy and diagnosis).—Veron, 1993: 339–340, fig. 53.

New Records

Umatuka Maru: stn 6927, 1, WAM 220–92.

Lady: stn RW96–5, 1, NTM C8061.

Other records: stn Pac, Mermaid Sound, Dampier Archipelago, 7–9 m, 13 II 1981, 2, WAM 342– and 343–88; stn pA5, *Ibid.*, 4 II 1981, 1, WAM 352–88; stn PE4–7, *Ibid.*, 12 II 1981, 1, WAM 381–88; stn

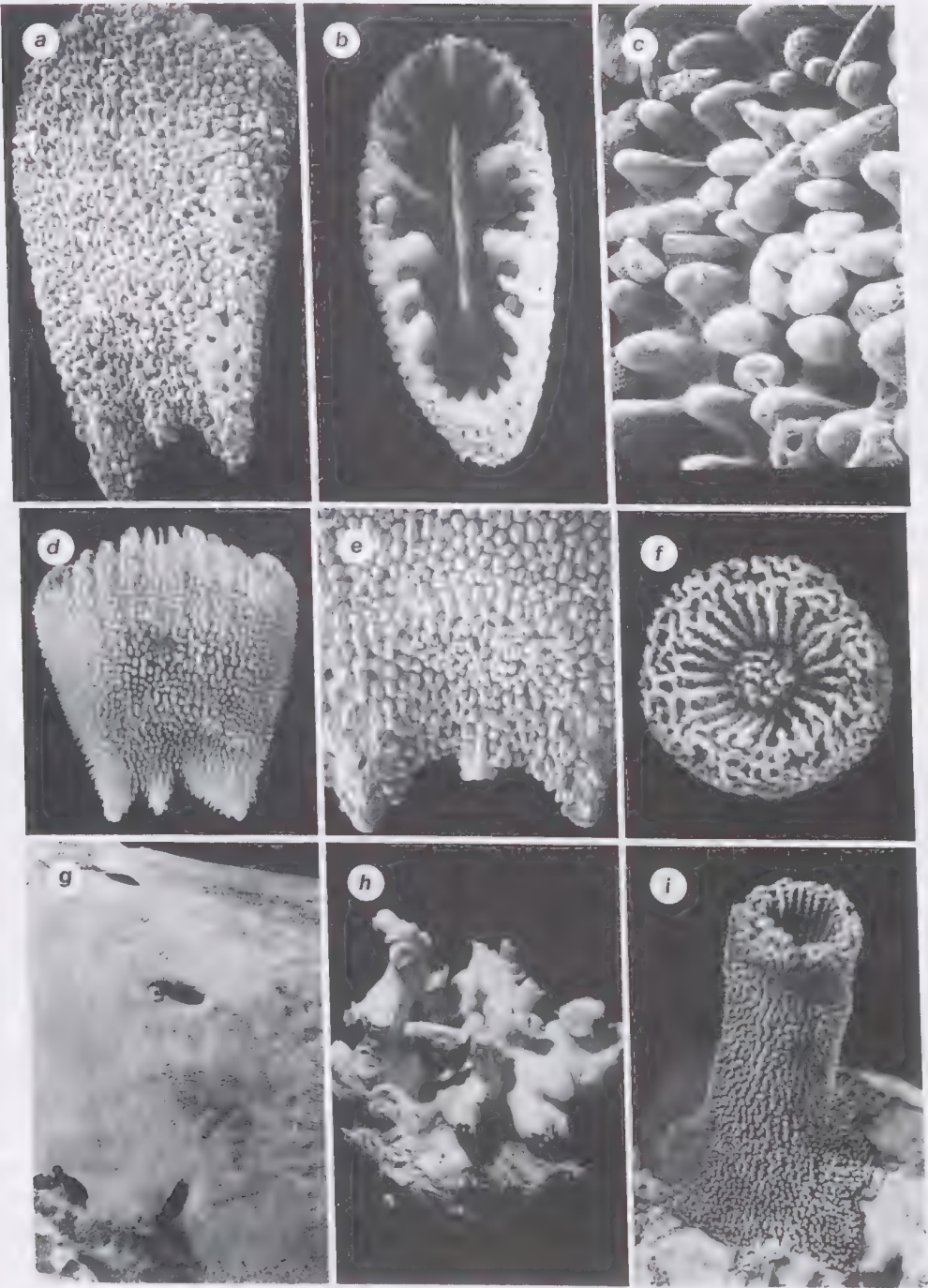


Figure 9 a-e, *Notophyllia piscacauda*, a-c, e, paratype from King George Sound, USNM 85715: a-b, side and calicular views, x 13; c, sand grains lodged between costal granules in basal scar region, x 83; e, "fishtail"-shaped basal scar region, x 15; d, holotype, x 6.7. f, i, *Leptopsammia columna*, holotype, SMNH 4756, calicular and side views, x 14, x 7.0, respectively. g, *Dendrophyllia alcocki*, Soela stn 01/84/55, WAM 561-84, base of colony penetrated by several acrothoracican cirripede burrows, x 2.8. h, *D. boschmai*, Soela stn 02/82/15, WAM 21-83, corallum, x 0.5.

SB3, 24°54'S, 113°17.8'E, 23 m, 2 V 1981, 2, WAM 700–81; stn Flinders 12, 28°39.5'S, 113°47.5'E, 37 m, 22 VIII 1977, 1, WAM 140–83; Port Essington, Cobourg Peninsula, Northern Territory, 1, NTM C8038.

Remarks

According to Veron and Pichon (1980:419), this species may be either zooxanthellate or azooxanthellate, the latter expanding its polyps only at night.

Distribution

Western Australia: continental shelf of western coast from Joseph Bonaparte Gulf to Abrolhos Islands; 9–137 m (Veron and Marsh 1988). Elsewhere: widespread in Indo-West Pacific; depth range not known (Veron and Pichon 1980; Hoeksema and Best 1991).

Genus *Rhizosammia* Verrill, 1870

Rhizosammia verrilli van der Horst, 1922

Rhizosammia verrilli van der Horst, 1922: 64–65, pl. 8, figs. 1–2.—Cairns, 1991: 25, pl. 11, figs. c–e (synonymy and description).—Cairns and Zibrowius, 1997: 188–189, figs. 28 f–g.

New Records

stn "12", Egeria Point, Christmas Island, 9–20 m, 19 II 1987, 1 colony, WAM 385–87; stn "13", Northwest Point, Christmas Island, 19 II 1987, 2 colonies, WAM 386–87; Lost Lake, Christmas Island, 1–2 m, 18 II 1987, 1 colony, WAM 384–87; 13°56'S, 125°37'E (Cassini Island, Kimberley), "SCUBA" depth, 18 VIII 1991, 1 colony, WAM 147–91; 20°28'30"S, 116°32'E, 26 V 1974, 3 colonies: 2 (WAM 10–76), 1 (USNM 96701); Ningaloo, Winderabandi, 5–12 m, 4 VIII 1985, 2 colonies, WAM 956–85; 26°10'10"S, 113°11'00"E, 2 m, 15 IV 1979, 7 colonies, WAM 451– and 552–79; stn C71, Leo Island, Abrolhos, 38 m, 1 IX 1972, 1 corallite, WAM 71–73.

Remarks

Living specimens are orange-pink to pale pink in colour. Other azooxanthellate species, such as *Culicia australiensis* and *Thalamophyllia tenuescens*, often encrust the same substrate as *R. verrilli*.

Distribution

Western Australia: continental shelf of western coast from Kimberley to Abrolhos Islands; Christmas Island; 2–38 m. Elsewhere: South Pacific, including Philippines, Indonesia, Pelau, Cocos Islands (eastern Pacific) and Galápagos Islands; 5–278 m (Cairns and Zibrowius 1997).

Genus *Dendrophyllia* Blainville, 1830

Dendrophyllia alcocki (Wells, 1954)

Figure 9g

Sclerhelia alcocki Wells, 1954: 465–466, pl. 177, figs. 1–2.

Dendrophyllia alcocki – Zibrowius, 1974a: 570–573, figs. 10–14.—Cairns, 1995: 126–127, pl. 43, figs. g–i, pl. 44, figs. a–b (synonymy and description).—Cairns and Zibrowius, 1997: 193.

New Record

Soela: stn 01/84/55, 1 colony, WAM 561–84.

Remarks

The specimen reported above bears 9 characteristic lenticular-shaped burrows of an acrothoracican cirripede crustacean, each burrow having an aperture 3.0–3.1 mm in length and 0.8–1.3 mm in width (Figure 9g). All burrows occurred on the encrusting base of the corallum, as well as in the calcareous substrate on which the coral was attached. Whereas these boring cirripedes have been reported previously from deep-water Scleractinia (Grygier and Newman 1985; Cairns and Zibrowius 1997), this is the first record of this parasitic association between an acrothoracican and *D. alcocki*.

Distribution

Western Australia: continental slope off Cape Leveque, Dampier Land; 296–298 m. Elsewhere: Indo-West Pacific from Maldiv Islands to New Zealand, including the Marshall Islands and South China Sea; 118–616 m (Cairns and Zibrowius 1997).

Dendrophyllia arbuscula van der Horst, 1922

Dendrophyllia arbuscula van der Horst, 1922: 53, pl. 8, fig. 6.—Wells, 1964: 108.—Cairns, 1994: 90–91, pl. 38, figs. i–l (synonymy and description); 1995: 125–126, pl. 43, figs. e–f.—Cairns and Zibrowius, 1997: 192–193, figs. 29 a–c.

Dendrophyllia – Veron, 1986: 578, in part: black and white fig.

New Records

Long Island, Wallabi Group, Abrolhos, 24–30 m, 16 IV 1978, 1 colony, WAM 207–78; Evening Reef, Abrolhos, 49 m, 2 colonies: 1 (WAM 172–81), 1 (USNM 96703); Sorrento, north of Fremantle, 5 m, IV 1971, 3 colonies, WAM 68–78; Armstrong Bay, Rottne Island, 1–2 m, 14 II 1985, 4 colonies, WAM 328–89.

Remarks

Living specimens are orange-red in colour.

Distribution

Western Australia: continental shelf of

southwestern coast from Abrolhos Islands to Rottneest Island; 2–49 m. Elsewhere: Indo-west Pacific from southwestern Indian Ocean to northern New Zealand, including Japan; 40–353 m (Cairns and Zibrowius 1997).

Dendrophyllia boschmai van der Horst, 1926

Figure 9h

Dendrophyllia boschmai van der Horst, 1926: 44.—Cairns, 1994: 91 (synonymy and diagnosis).

New Records

Soela: stn 02/82/14, 1 branch, WAM 19–83; stn 02/82/15, 1 large colony and 2 branches: colony and 1 branch (WAM 21–83), 1 branch (USNM 96706).

Distribution

Western Australia: northwestern coast off Port Hedland; 200–201 m; 16.0°–16.3°C. Elsewhere: previously known only from off Japan and South Korea; 40–165 m (Cairns 1994).

Dendrophyllia spp.

Dendrophyllia sp. – Veron, 1986: 579, fig. 4.—Grygier, 1991: 42, figs. 21 D–E.

Records

Kendrew Island, Dampier Archipelago, 4 m, 5 VIII 1978, 1, WAM 412–78; Mangrove Bay, North West Cape, 13 m, 26 V 1980, 1, WAM 63–81; Long Island, Wallabi Group, Abrolhos, 6–30 m, 11–16 IV 1978, 3, WAM 204–, 205–, and 206–78; Ibid., Beacon Island, V 1978, 1, WAM 602–78; Hopetoun jetty, 12 I 1986, 1, WAM 415–86.

Remarks

Like *Balanophyllia*, the taxonomy of the 24 Recent species (Best et al. 1995) of *Dendrophyllia* is in need of revision. Specimens unidentified to species occur from Dampier Archipelago to Hopetoun at depths of 4–30 m.

Genus *Tubastraea* Lesson, 1829

Tubastraea coccinea Lesson, 1829

Tubastraea coccinea Lesson, 1829: 93.—Wells, 1983: 243–244, pl. 18, figs. 1–2 (synonymy).—Veron, 1986: 580–581 (2 figs.).—Ogawa and Takahashi, 1993: 98, pl. 1, figs. 1–8, pl. 2, figs. 1–4, pl. 5, figs. 1–5.—Cairns, 1994: 93–94, pl. 39, figs. g–i (synonymy and description).—Cairns and Zibrowius, 1997: 197.

Tubastrea aurea – Wells, 1964: 109.—Veron, 1986: 584, fig. 1.

New Records

Stn "16", 13°56'S, 125°37'E, 17 VIII 1991, 1, WAM 148–91; stn "35", 15°21'S, 123°32'E, 24 VIII 1991, 1, WAM 155–91; Kendrew Island, Dampier Archipelago, 3–8 m, 1971–1978, 5, WAM 48–72, 128–73, 69– and 411–78, and NMV F78384; stn "142", Hermide Island, Monte Bello Islands, 3–4 m, 12 XII 1979, 1, WAM 392–80; Yardie Creek, North West Cape, 19 VI 1977, 1, WAM 211–77; Ningaloo, North West Cape, VIII 1973, 1, WAM 70–78; stn BI9, Cape Couture, Bernier Island, 1 m, 10 III 1980, 1, WAM 116–81; Dirk Hartog Island, 4 m, 30 V 1957, 3, WAM 16– and 23–59; Monkey Rock, Shark Bay, 2–3 m, 4 IV 1979, 1, WAM 455–79; 26°10'20"S, 113°11'W, 2 m, 11 IV 1979, 1, WAM 550–79; Wallabi Group, Abrolhos Islands, 9 m, 13 IV 1978, 1, WAM 140–78; stn C31, Easter Group, Abrolhos Islands, 0.3 m, 30 VIII 1972, 1, WAM–31–73; Cockburn Sound, XI 1957, 1, WAM 465–78; Carnac Island, 2–3 m, 9 XII 1977, 2, WAM 192–78; Rottneest Island, 1956–1985, 1–2 m, 7: WAM 141–58, 139–58, 64–78, and 88–85, USNM 83687, USNM 83689, and NMV F78386; Little Armstrong Bay, Rottneest Island, roof of cave, 3–5 m, 5 II 1993, 1 colony, SAM H876.

Remarks

Living specimens are bright orange in colour (Veron 1986).

Distribution

Western Australia: continental shelf of western coast from Cassini Island to Rottneest Island; 0.3–20 m; common in caves and under ledges. Elsewhere: cosmopolitan in tropical and warm temperate waters; 1.5–110 m (Cairns and Zibrowius 1997).

Tubastraea diaphana (Dana, 1846)

Dendrophyllia diaphana Dana, 1846: 389, pl. 27, fig. 3.

Tubastraea diaphana – Wells, 1964: 108.—Veron, 1986: 582 (fig. 2), 585 (center unnumbered fig.).—Ogawa and Takahashi, 1993: 99, pl. 2, figs. 9–10, pl. 5, fig. 7.—Cairns and Zibrowius, 1997: 196–197 (synonymy and diagnosis).

New Records

Kendrew Island, Dampier Archipelago, 2–9 m, 1972–1974, 9 colonies, WAM 165–, 257–, and 173–73, 92–74; Hermite Island, Monte Bello Islands, 11 XII 1979, 1, WAM 390–80; Mandu Mandu, North West Cape, 22 V 1980, 1, WAM 200–81; Yardie Creek, North West Cape, 20 VI 1977, 1, WAM 213–77; 21°51'50"S, 116°09'30"E, 2–4 m, 29 V 1981, 1, WAM 587–81; Ningaloo, 0–1 m, 6 VIII 1985, 2, WAM 936–85; Bernier Island, Cape Couture, 10 III 1980, 2, WAM 110–81; Dirk Hartog Island, 0–1 m, 5 IV 1979, 2, WAM 17–59 and 453–79; South Pass, Shark Bay, 12 m, 15 IV 1979, 1, WAM 558–79; stn "11", 26°08'30"S, 113°08'10"E, 8 IV 1979, 1, WAM 563–79;

Long Island, Wallabi Group, Abrolhos Islands, 3–30 m, IV 1978, 7 colonies, WAM 193–, 194–, 197–, 198–, 200–, 202–, and 203–78; Beacon Island, Wallabi Group, Abrolhos Islands, 23 IV 1974, 3, WAM 66–78; Ibid., 31 m, 1, WAM 479–77; Easter Group, Abrolhos Islands, 0.2 m, 30 VIII 1972, 1, WAM 52–73; Green Head, 4 m, VI 1979, 1, WAM 969–79; Little Island, Sorrento, 14 XII 1977, 3, WAM 196–78; Cockburn Sound, IX 1957, 2, WAM 464–78; Rottneest Island, 1956, 1, WAM 138–58.

Remarks

Living specimens are black to dark green in colour (Veron 1986).

Distribution

Western Australia: continental shelf of western coast from Dampier Archipelago to Rottneest Island; 0–30 m; common in caves, on vertical walls, and under ledges. Elsewhere: widespread in tropical Indo-west Pacific from southwestern Indian Ocean to Fiji; 1–54 m (Cairns and Zibrowius 1997).

Tubastraea micranthus (Ehrenberg, 1834)

Oculina micranthus Ehrenberg, 1834: 304.

Tubastraea micranthus – Schuhmacher, 1984: 94, figs. 1a–b, 4.—Cairns and Zibrowius, 1997: 195–196 (synonymy and description).

Tubastrea micrantha – Wells, 1964: 108.—Veron, 1986: 583 (fig. 3), 585 (figs. 3, 7).—Ogawa and Takahashi, 1993: 99–100, pl. 4, figs. 1–6, pl. 6, figs. 5–6.

New Records

Stn “11”, Ashmore Reef, 10–20 m, 15 VIII 1986, 1, WAM 593–86; Kendrew Island, Dampier Archipelago, 6–9 m, 23 V 1972, 1 branch, WAM 49–72; stn “ML3”, Noname Bay (20°36'S, 116°45.5'E), Dampier Archipelago, 4–6 m, 1, WAM 413–78.

Remarks

Living specimen are black to dark green-black in colour (Veron 1986).

Distribution

Western Australia: Ashmore Reef and Dampier Archipelago; 6–10 m. Elsewhere: widespread in tropical Indo-West Pacific from southwestern Indian Ocean to Fiji; 0–60 m (Cairns and Zibrowius 1997).

ACKNOWLEDGEMENTS

I would particularly like to thank Loiset Marsh (WAM), who first suggested this project and who graciously made the WAM specimens available to me for study. Mark J. Grygier was also an encouragement to begin and continue the work.

I would like to thank the following people who have generously loaned me specimens used in this study: Phil Alderslade (NTM), Karin Sindemark (SMNH), Timothy Stranks (NMV), Wolfgang Zeidler (SAM), and Penny Berents (AMS).

The scanning electron photomicrographs were taken in the SEM Laboratory of the National Museum of Natural History.

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STATION LIST

	Latitude (°S)	Longitude (°E)	Depth (m)	Date	Temperature (°C)
<i>RV Akademik Oparin</i>					
unnumbered	19°19.7'	119°09.8'	50	19 VII 1987	
<i>Alpha Helix</i>					
M-14	11°33.5	135°52.5	22	2 VI 1979	
<i>FV Courageous</i>					
001	17°25'	119°52'	300-432	14 VIII 1983	
002	18°05'	118°10'	400-401	17 VIII 1983	
003	18°01'	118°13'	450-452	17 VIII 1983	
004	18°06.5'	118°10'	353-356	17 VIII 1983	
011	16°53'	119°53'	339-438	19 VIII 1983	
013	16°49'	119°59'	439-468	19 VIII 1983	
?015	16°50'	120°03'	433-434	20 VIII 1983	
017	16°58'	120°07'	428-432	20 VIII 1983	
018	16°56'	120°06'	431	20 VIII 1983	
020	17°49'	118°41'	308-310	21 VIII 1983	
022	17°55'	118°22'	437-442	21 VIII 1983	
023	17°57'	118°19'	431-433	21 VIII 1983	
025	18°02'	118°14'	409-410	22 VIII 1983	
026	18°05'	118°08'	440-442	22 VIII 1983	
033	18°34'	117°17'	475-477	23 VIII 1983	
090	16°42'	120°10'	390	4 IX 1983	
<i>DEKI</i>					
3	5°32'	132°36'	245	31 III 1922	
<i>HMAS Diamantina</i>					
20	31°44'	114°56'	402-448	16 III 1976	
25	31°48'	114°58'	402	16 III 1976	
45	31°00'	114°51'	80	17 III 1976	
55	29°15'	114°01'	146	20 III 1976	
76	31°30'	114°56'	146	23 III 1972	
92	26°30'	112°54.2'	146	7 XII 1970	
173	21°50'	113°46'	137	6 X 1963	
185	23°25'	113°14'	?	7 X 1963	
186	23°23'	113°09'	278	7 X 1963	
208	27°40'	113°20'	130	10 X 1963	
<i>O.R.V. Franklin</i>					
GAB033	33°00'	128°00'	83	17 VII 1995	
GAB042	33°26'	125°58'	234	18 VII 1995	
GAB063	32°52'	125°04'	46	20 VII 1995	
<i>MV Espiritu Santo</i>					
E68-743	19°29'	116°01'	137	1 XII 1968	
<i>Hai Kung</i>					
MFG81	19°35'	117°15'	73-80	10 III 1981	
<i>Hokuho Maru</i>					
KH72-1-30	12°24.8'	128°00.1'	115	25 VI 1972	
<i>KARUBAR</i>					
44	7°52'27"	132°48'24"	291-295	29 X 1991	
49	7°59'51"	132°58'50"	206-209	29 X 1991	
65	9°14'01"	132°28'28"	174-176	1 XI 1991	
86	9°23'59"	131°14'29"	222-226	4 XI 1991	
<i>MV Kunmunyah</i>					
BG 2	13°27.96'	129°56.10'	7	1 X 1993	
BG 13	13°22.14'	129°53.40'	24	2 X 1993	
BG 20	13°19.14'	129°56.28'	29	2 X 1993	
BG 21	13°19.14'	129°56.10'	31	2 X 1993	
BG 26	13°16.08'	129°55.92'	23	3 X 1993	

	Latitude (°S)	Longitude (°E)	Depth (m)	Date	Temperature (°C)
BG 27	13°15.90'	129°58.86'	19	3 X 1993	
BG 28	13°15.90'	130°01.86'	20	2 X 1993	
BG 36	13°10.26'	129°55.62'	15	3 X 1993	
BG 39	13°07.08'	129°56.04'	15	3 X 1993	
BG 46	13°00.90'	129°58.92'	14	4 X 1993	
BG 47	13°00.96'	130°01.92'	17	4 X 1993	
BG 56	12°52.02'	130°11.10'	6	4 X 1993	
BG 77	12°33.60'	130°27.90'	16	6 X 1993	
BG 80	12°31.02'	130°17.22'	17	5 X 1993	
BG 82	12°30.96'	130°22.92'	9	6 X 1993	
BG 83	12°31.02'	130°28.98'	28	6 X 1993	
BG 86	12°27.78'	130°22.98'	13	6 X 1993	
BG 91	12°25.44'	130°25.92'	19	6 X 1993	
BG101	12°19.02'	130°34.02'	19	7 X 1993	
BG141	12°07'02"	130°07'02"	20	10 X 1993	
<i>R/V Lady</i>					
RW96-5	14°12.8'	128°41.3'	32	10 VI 1996	
RW96-7	13°21.02'	128°10.44'	77	10 VI 1996	
RW96-8	12°52.66'	127°53.06'	100	13 VI 1996	
RW96-14	12°59.09'	124°43.65'	80	12 VI 1996	
RW96-17	12°42.86'	123°57.98'	180	13 VI 1996	
RW96-18	12°43.08'	123°33.21'	280	13 VI 1996	
RW96-19	12°43.00'	123°28.59'	350	13 VI 1996	
RW96-29	13°06.44'	123°15.43'	400-420	19 VI 1996	
RW96-30	13°07.89'	123°12.65'	420	19 VI 1996	
RW96-31	13°39.09'	123°07.05'	350	19 VI 1996	
<i>R/V Lady Basten</i>					
LB1b(s)	20°10'	116°58.5'	45	17 VIII 1995	
LB3(t)	19°29.7'	117°26.6'	78	17 VIII 1995	
LB4(s)	19°08.4'	117°44'	112-124	17 VIII 1995	
LB5(s)	18°42.8'	118°03.2'	150-160	18 VIII 1995	
LB5(t)	18°36.6'	118°07'	150-160	18 VIII 1995	
LB6(s)	18°06.9'	118°56.7'	173-193	18 VIII 1995	
LB6(t)	18°09.5'	118°54.5'	173-193	18 VIII 1995	
LB7(s)	17°54.2'	116°17.5'	200	18 VIII 1995	
LB8(t)	17°48.7'	119°22.3'	250	18 VIII 1995	
<i>FV Longva III</i>					
"1"	38°18'	124°43'	945-1220	8 XII 1989	
"2"	34°13'	125°01'	912-963	8 XII 1989	
<i>HMS Moresby</i>					
12	14°36.9'	128°47.8'	?	30 IX 1980	
14	14°35.2'	128°55.2'	?	30 IX 1980	
<i>FV Saxon Progress</i>					
RP-8	34°45'	119°32.4	525-550	18 VIII 1988	
<i>Soela 01/79</i>					
unnumbered	19°34'	116°08'	101	19 VIII 1979	
18	19°32'	116°00'	144	3 XII 1979	
66	20°57'	115°40'	12	10 XII 1979	
69	20°50'	115°40'	16	10 XII 1979	
<i>Soela 02/82</i>					
9	18°33'	118°22'	150	28 III 1982	19.0°
10A	18°47'	117°58'	154	28 III 1982	
10B	18°47'	117°58'	?	29 III 1982	
12A	19°29'	118°22'	56	1 IV 1982	
13A	18°25'	118°22'	201	2 IV 1982	
14	18°31'	118°09'	200-201	2 IV 1982	16.3°
15	18°40'	117°53'	200	2 IV 1982	16.0°
16	18°41'	117°54'	200-204	2 IV 1982	16.2°
17A	18°01'	118°17'	410-420	3 IV 1982	

	Latitude (°S)	Longitude (°E)	Depth (m)	Date	Temperature (°C)
17	17°48.1'	118°30'	404	3 IV 1982	9.6°
18	18°08'	118°06'	404	3 IV 1982	9.6°
19	18°35'	117°00'	588-592	4 IV 1982	8.5°
21	18°45'	116°26.5'	590-592	4 IV 1982	9.0°
22	18°40'	116°27.5'	720-724	5 IV 1982	8.4°
26	18°37'	116°46'	696-700	6 IV 1982	10.0°
27	18°41'	116°29.5'	696-704	6 IV 1982	8.7°
28	18°41'	116°44'	594-596	6 IV 1982	
29	18°43'	116°35'	610-612	7 IV 1982	8.2°
31	18°41'	116°56'	500	7 IV 1982	7.8°
34	18°29'	117°32'	496-500	8 IV 1982	8.2°
35	17°34'	118°38'	472-520	10 IV 1982	8.5°
38	18°22'	117°56'	309-316	10 IV 1982	10.0°
40	18°34'	117°40'	304	11 IV 1982	10.7°
41	18°26'	117°34'	416-418	11 IV 1982	9.6°
43	18°40'	117°13'	300-306	13 IV 1982	12.0°
45	18°49'	116°50'	400-406	13 IV 1982	9.1°
46	18°41'	116°45'	506-508	13 IV 1982	8.5°
51	19°13'	117°39'	100	15 IV 1982	23.1°
54	19°15'	116°59'	152-156	15 IV 1982	
54A	19°59'	117°16'	50-52	15 IV 1982	28.8°
Soela 04/82					
8A	18°55'	116°41'	380	1 VIII 1982	19.0°
8B	18°46'	117°41'	360	1 VIII 1982	
8C	18°43'	117°12'	368	1 VIII 1982	
51A	20°10'	116°34'	49	15 VIII 1982	
64	19°25'	117°11'	90-98	17 VIII 1982	
71	18°30.1'	118°36.2'	136-146	19 VIII 1982	
74	18°43'	118°17'	144	19 VIII 1982	
76A	18°57'	118°28'	95	19 VIII 1982	
Soela 05/82					
12	20°01'	117°13.1'	46-49	27 IX 1982	
13	19°52.3'	117°16.1'	56-58	27 IX 1982	
22	20°34'	116°06.4'	28-30	29 IX 1982	
27	19°51.8'	116°30'	62	29 IX 1982	22.9°
36	19°10'	116°57.2'	180-190	1 X 1982	17.4°
37	19°19.2'	116°46.3'	132-144	1 X 1982	21.5°
42	18°58'	117°36.2'	140-164	2 X 1982	23.5°
46	19°01.7'	117°59.3'	102-106	2 X 1982	
47	18°39.3'	118°57'	128-130	3 X 1982	22.8°
51	19°03'	118°15'	74-83	3 X 1982	
55	19°08.9'	118°46'	81-82	4 X 1982	
59	19°36.2'	118°39.3'	33-34	5 X 1982	
60	19°28.1'	118°27.1'	62.66	5 X 1982	24.1°
61	19°31.2'	118°06.9'	65-68	5 X 1982	
63	19°34.2'	117°57.4'	60-65	5 X 1982	23.9°
65	19°34.0'	117°18.3'	78-84	6 X 1982	23.5°
71	19°53'	117°55'	40	7 X 1982	
Soela 01/84					
24	18°41'	117°28'	304	1 II 1984	
49	16°58.7'	119°55.6'	430-432	9 II 1984	
51	15°40.2'	120°37.3'	500-504	10 II 1984	
52	15°46.4'	120°39.9'	446-450	10 II 1984	
53	15°48'	120°41'	396-400	10 II 1984	
54	15°51.2'	120°44.3'	348-350	10 II 1984	
55	15°57'	120°46.2'	296-298	10 II 1984	
56	15°20'	121°11.2'	300-302	11 II 1984	
57	15°13.5'	121°08.9'	352	11 II 1984	
59	15°09.4'	121°05.5'	448-450	11 II 1984	
60	15°08.6'	121°05.4'	500-504	11 II 1984	
61	14°39.5'	121°28.5'	500-506	12 II 1984	
63	14°43.1'	121°33.1'	408-410	12 II 1984	
64	14°50.2'	121°31.4'	356	12 II 1984	

	Latitude (°S)	Longitude (°E)	Depth (m)	Date	Temperature (°C)
65	14°49'	121°36.1'	300-302	12 II 1984	
66	14°29.4'	122°01.4'	296-304	12 II 1984	
67	14°21.5'	122°02.4'	348-350	12 II 1984	
70	13°44'	122°13.3'	494-496	13 II 1984	
71	13°50.3'	122°18.5'	450-452	13 II 1984	
72	14°07.5'	122°29.4'	406-408	13 II 1984	
74	14°16.5'	122°34.4'	302	14 II 1984	
75	13°51.4'	123°01.8'	306-308	14 II 1984	
76	13°44.5'	122°56.5'	348-350	14 II 1984	
77	13°33.3'	122°51.5'	390-394	14 II 1984	
78	13°27.6'	122°44.4'	440-444	14 II 1984	
79	13°17'	122°37.4'	484-494	15 II 1984	
80	12°48.1'	122°56.7'	496-504	15 II 1984	
81	12°54.4'	123°00.2'	452-463	15 II 1984	
82	13°07.2'	123°15.7'	400	15 II 1984	
82A	14°35.8'	121°49.4'	300-304	16 II 1984	
85	14°52.5'	121°41.7'	220-224	16 II 1984	
87	15°11.1'	121°26.9'	258-260	17 II 1984	
91	16°08'	120°19.5'	544-550	18 II 1984	
92	16°09.5'	120°08.8'	596-600	18 II 1984	
94	16°55.8'	119°53.9'	426	19 II 1984	
96	16°55.4'	119°54.1'	431-432	19 II 1984	
98	16°56.7'	119°51.2'	432	20 II 1984	
99	16°56.8'	119°51'	430-432	20 II 1984	
100	16°55.9'	119°52'	432-436	20 II 1984	
101	16°56.9'	119°50.9'	432	20 II 1984	
102	16°55.2'	119°52.8'	430-432	20 II 1984	
105	16°56.9'	119°52'	432	21 II 1984	
107	16°55.2'	119°54.9'	432	21 II 1984	
108	16°54.1'	119°55.6'	434	21 II 1984	
109	16°54.1'	119°54.2'	433-434	22 II 1984	
111	16°55.1'	119°54.8'	430-432	22 II 1984	
112	16°55'	119°56'	432-434	22 II 1984	
113	16°57'	119°51'	436	22 II 1984	
116	16°55.4'	119°52.3'	436-448	23 II 1984	
118	16°54'	119°52'	440	23 II 1984	
119	16°51'	119°48'	464-466	23 II 1984	
120	18°01'	118°11'	530-560	24 II 1984	
121	18°04'	118°14'	396-400	24 II 1984	
122	17°59'	118°23'	389-390	24 II 1984	
<i>MV Sprightly</i>					
19M	29°14'	114°04'	165	17 II 1976	
20M	29°21'	114°07'	146	18 II 1976	
28M	29°08.5'	113°54.8'	183	19 II 1976	
30M	29°07.5'	113°57.4'	110	19 II 1976	
33M	29°06.7'	113°58.5'	91	19 II 1976	
34M	29°07.2'	113°56.4'	141	19 II 1976	
35M	29°07.5'	114°10'	64	19 II 1976	
40M	30°15.9'	114°38.6'	137	19 II 1976	
41M	30°16.8'	114°39.6'	82	19 II 1976	
SP4/82/41	15°40.7'	122°13.9'	40	28 IV 1982	
<i>FV Surefire</i>					
5	18°46'	116°24'	?	7 II 1992	
<i>Umatuka Maru</i>					
6920	S of Rowley Shoals		260	20 XII 1969	
6921	S of Rowley Shoals		300	20 XII 1969	
6922	S of Mermaid Reef, Rowley		340	20 XII 1969	
6926	S of Rowley Shoals		266	20 XII 1969	
6927	W of Broome		90	21 XII 1969	
6930	NW of Browse Island		380	23 XII 1969	

New *Euryglossa* (*Euhesma*) bees (Hymenoptera: Colletidae: Euryglossinae) associated with the Australian plant genus *Eremophila* (Myoporaceae)

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Abstract – Twenty species of *Euryglossa* (*Euhesma*) bees are described as new: *E. (E.) alicia*, *E. (E.) atra*, *E. (E.) aurata*, *E. (E.) balladonia*, *E. (E.) coppinensis*, *E. (E.) cuneifolia*, *E. (E.) granitica*, *E. (E.) macrayae*, *E. (E.) nalbarra*, *E. (E.) newmanensis*, *E. (E.) pantoni*, *E. (E.) scoparia*, *E. (E.) sturtiensis*, *E. (E.) sulcata*, *E. (E.) symmetra*, *E. (E.) walkeri*, *E. (E.) wiluna*, *E. (E.) yellowdinensis*, *E. (E.) leonora*, *E. (E.) meeka*. All are endemic Australian species collected from species of the native plant genus *Eremophila* and exhibit modified labial palps. Line drawings, scanning electron micrographs and a key enable the separation of all species. Distributions are mapped.

INTRODUCTION

Euryglossine bees are widespread in Australia and most are associated with the plant family Myrtaceae. It is now apparent that large numbers of undescribed species in the subgenus *Euhesma* Michener of the genus *Euryglossa* Smith have been collected on flowering non-Myrtaceous native plants. Many show modification of the head and mouthparts presumably as food plant adaptation. Interest in pollination mechanisms of Australian native plants has grown with the ability to make accurate identifications. Recently collected bees often bear the specific name of the flowers from which they were caught.

Examination of hundreds of *Euhesma* specimens suggest many species may be associated with specific plant species. Houston (1992) described three such species from Western Australia. It is unfortunate that all bees in collections don't carry full details but many are recorded from *Eremophila* species (Myoporaceae). This Australian plant genus of about 200 species occurs mainly in arid areas of the continent.

Dr Houston has collected widely in the huge state of Western Australia and from almost every site a different *Euhesma* species was taken on *Eremophila*. Whether the plant in each site was always a different species is not known, but *Eremophila* species are mainly shrubs with flowers that can be readily watched and, after this study, with accurate identification of both plant and bees now possible, it is hoped pollination studies will be encouraged.

In this paper, although only closely similar *Euhesma* species recorded from *Eremophila* are dealt with, they are not considered monophyletic. Based on the form of the labial palps 20 species collected from *Eremophila* spp. can be identified and these

form three groups. Males have not been collected as often as females and sex association is not always clear so the key presented is for females only.

Houston (1983) mentioned collecting many *Euhesma* with enlarged labial palps from bluish-flowered *Eremophila* species and interspecific variation relates in the main to the development of the labial palps and head length. The head may be lengthened behind the ocelli or the clypeus may be extended well beyond the level of the eyes. There is usually a clear malar space (unknown in most Euryglossinae). The whole labio-maxillary complex may be elongate or various segments of the labial palps enlarged (Figures 1-7). Apart from head shape and labial palps the species described below look very similar and some show only small structural differences concerning texture of frons or clypeus. Whether these indeed indicate species will only be known when more specimens, particularly males, become available.

METHODS

In the descriptions of species, 'relative head measurements' express most concisely the size relation between measurements on one head. Most of the specimens were coated with pollen or nectar, or were initially preserved in ethyl alcohol. Characters are obscured and some descriptions are not as complete as others.

Although the first criterion for inclusion in this paper is "collected from *Eremophila*", 3 specimens recorded here were taken elsewhere: one specimen of *E. (E.) yellowdinensis* from *Melaleuca*; and two specimens of *E. (E.) walkeri* from *Eucalyptus* sp.

All species names are to be treated as nouns in apposition to *Euhesma*.

- Group 2. Eight species with enormously extended labial palps in which segments 1 and 2 are short and dark brown and segments 3 and 4 are

The specific name relates to the dull black colour of head and thorax.

Euryglossa (Euhesma) aurata sp. nov.

Figure 49

Material Examined*Holotype*

♀, 35 km E of Norseman, Western Australia, 32°12'S 122°04'E, 30 October 1989, K.L. Walker on *Eremophila* (MV).

Paratypes

Australia: Western Australia: 1♀, 3♂ same data as holotype (MV).

Description*Female*

Length about 5.0 mm; wing length about 4.0 mm. Relative head measurements: width 6.3; length 7.1; clypeal length 1.9; lower interocular distance 3.7; upper interocular distance 4.3; interantennal distance 1.3; antennocular distance 0.7; interocellar distance 1.5; ocellocular distance 1.2. Clypeus with anterior margin indented medianly, upper margin slightly concave, dorsum shining with median longitudinal furrow; labial palps with segments in increasing lengths in the order 2, 1 = 3, 4. Labial palp segment one dark brown, others yellowish; legs dark brown with tibiae and tarsi mostly golden; dorsal surface of gaster golden brown with wide bands across segments 1–3 dark brown; venter light brown.

Forewing with first recurrent vein distal to first transverse cubital.

Male

Length about 4.0 mm; wing length about 3.0 mm. Relative head measurement: width 5.5; length 5.6; clypeal length 1.2; lower interocular distance 2.9; upper interocular distance 4.1; interantennal distance 0.9; antennocular distance 0.7; interocellar distance 1.4; ocellocular distance 1.1; ocellocipital distance 0.1. Clypeus as in ♀; labial palps with segments in increasing lengths in the order 2, 3, 1, 4.

Labial palp segments 1, 2 dark brown, 3, 4 yellowish; legs dark brown with fore tibiae and all tarsi light brown.

Forewing with first recurrent vein interstitial with first cubital. Long white hairs on head, especially on clypeus.

Remarks

The males described are very much smaller than others in this group. They differ from the females in that colour is black predominantly and the first recurrent vein of the forewing is interstitial with the first cubital.

Etymology

The specific name refers to the golden brown colour on the gaster and legs of the female.

Euryglossa (Euhesma) balladonia sp. nov.

Figures 37, 46, 49

Material Examined*Holotype*

♀, 32°12'S 123°18'E, 35 km NW by W Balladonia RH, Western Australia, 18 September 1981, I.D. Naumann and J.C. Cardale, on flowers of *Eremophila* (ANIC).

Paratypes

Australia: Western Australia: 1♀, 1♂ same data as holotype (ANIC).

Other Material

Australia: Western Australia: 7♀, 2♂, 32°27'S 121°41'E, 30 km SSW of Norseman, 19 September 1981, I.D. Naumann and J.C. Cardale, (ANIC).

Description*Female*

Length about 5.5 mm; wing length about 4.0 mm. Relative head measurements: width 7.4; length 7.7; clypeal length 2.3; lower interocular distance 4.3; upper interocular distance 5.0; interantennal distance 1.7; antennocular distance 1.1; interocellar distance 1.6; ocellocular distance 1.0; ocellocipital distance 0.1. Upper margin of clypeus straight; labial palps with segments in increasing lengths 2, 1, 3, 4; fronto-clypeal suture distinct; clypeus not smooth, but with a low sheen.

Labial palp segments 1 and 2, dark brown, 3 and 4 golden brown (all dark brown in specimens from Norseman).

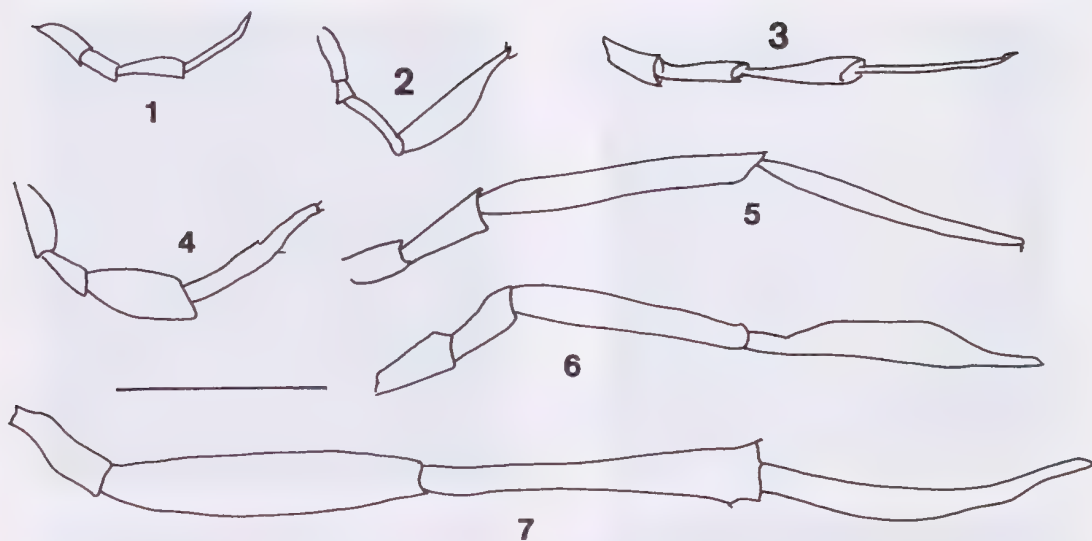
Forewing with first recurrent vein interstitial with first transverse cubital.

Male

Length about 5.0 mm; wing length about 4.0 mm. Relative head measurements: width 7.0; length 7.0; clypeal length 2.0; lower interocular distance 3.8; upper interocular distance 4.5; interantennal distance 1.2; antennocular distance 0.8; interocellar distance 1.6; ocellocular distance 0.9. Antennae long, middle flagellar segments longer than wide; basitibial plate indicated by carina and tubercles with terminal tubercle about 1/3 along hind tibia.

Forewing with first recurrent vein interstitial with first transverse cubital.

Seventh gastral sternum (Figure 37) with branched hairs on all 4 lobes. Eighth gastral sternum (Figure 46) with branched hairs laterally on distal shaft.



Figures 1-7 Labial palps of female *Euryglossa* (*Euhesma*) species collected on flowers of *Eremophila* species. 1, *E. leonora*; 2, *E. scoparia*; 3, *E. nalbarra*; 4, *E. symmetra*; 5, *E. meeka*; 6, *E. sulcata*; 7, *E. macrayae*. Scale line = 0.5mm.

Remarks

This is the only species in which the antennae of males are longer than usual with the middle flagellar segments longer than wide.

Etymology

The specific name refers to the type locality.

Euryglossa (*Euhesma*) *leonora* sp. nov.

Figures 1, 22, 23, 33, 42, 49

Material Examined

Holotype

♀, 50 km E of Leonora, Western Australia, 28°51'S 121°50'E, 10 September 1982, B. Hanich and T.F. Houston, on flowers of *Eremophila pantonii* (WAM).

Paratypes

Australia: Western Australia: 1♀, same data as holotype (WAM).

Other Material

Australia: Western Australia: 1♀, 9♂, 4 miles (6.4 km) NE of Menzies, 2 September 1971, T.F. Houston, on blue *Eremophila* (WAM).

Description

Female

Length about 5.5 mm; wing length about 4.0 mm. Relative head measurements: width 7.4; length 8.0;

lower interocular distance 4.3; upper interocular distance 4.9; interantennal distance 1.4; antennocular distance 0.9; interocellar distance 1.9; ocellocular distance 1.2; ocelloccipital distance 0.1. Anterior margin of clypeus broadly truncate; labial palps slightly longer than maxillary palps with segments in increasing lengths in the order 2, 1, 3, 4 (Figure 1); malar space short; horizontal zone of propodeum longer than metanotum; clypeus shining with punctures wide apart; frons above antennae dull.

Head black with antennal flagella yellowish ventrally; labial palps with segments 1, 2 dark brown, segments 3 and 4 light brown with basal parts dark brown; legs dark brown with fore tibiae anteriorly and all tarsi yellowish.

Forewing with first recurrent vein interstitial with first transverse cubital.

Scattered long white hairs on frons, clypeus, vertex, mandibles, posterior genae, sides of thorax, legs, venter, gastral tergum 5.

Male

Length about 4.5 mm; wing length about 3.7 mm. Relative head measurements: width 5.1; length 5.1; clypeal length 1.5; lower interocular distance 2.6; upper interocular distance 3.5; clypeo-antennal distance 0.3; interantennal distance 0.9; antennocular distance 0.6; interocellar distance 1.3; ocellocular distance 0.9; ocelloccipital distance 0.1. Labial palps and forewings as in female; inner hind tibial spur finely pectinate; horizontal zone of propodeum sloping, longer than metanotum; frons above antennae dullish with close reticulation and close punctures.

Terminalia (Figures 22, 23, 33, 42). The seventh gastral sternum (Figure 33) seems quite unlike any others examined.

Etymology

The specific name refers to the type locality.

Euryglossa (Euhesma) nalbarra sp. nov.

Figures 3, 10, 14, 20, 21, 31, 32, 40, 41, 49

Material Examined

Holotype

♀, 7 km W. Nalbarra HS, Western Australia, 28°39'S 117°36'E, 29–30 August 1981, T.F. Houston, on flowers of *Eremophila* aff. *georgei* (WAM).

Paratypes

Australia: Western Australia: 10♀, 2♂, same data as holotype (WAM); 10♀, 4♂, 26 miles (41.6 km) SSE of Wiluna, 1 November 1971, T.F. Houston, on blue *Eremophila* (WAM); 1♀, 9 km ENE of Anketell HS, 28°02'S 118°51'E, 3–6 September 1981, T.F. Houston, on flowers of *Eremophila* cf. *spinosa* (WAM).

Description

Female

Length about 7.0 mm; wing length about 5.0 mm. Relative head measurements: width 8.6; length 10.1; clypeal length 3.9; lower interocular distance 5.5; upper interocular distance 5.8; interantennal distance 1.8; antennocular distance 1.2; interocellar distance 2.1; ocellocular distance 1.5; ocelloccipital distance 0.8. Anterior margin of clypeus indented medianly, upper margin of clypeus concave; malar space distinct, labial palps longer than maxillary palps with segments in increasing lengths 1 = 2, 3, 4, all segments subcylindrical (Figures 3, 14); horizontal zone of propodeum sloping, longer than metanotum; clypeus shining with punctures wide apart; foveae of 2nd segment of gaster about twice as long as wide.

Head black, antennae with scapes and pedicels black, flagella black dorsally, yellowish ventrally; labial palps with segments 1 and 2 dark brown, segments 3 and 4 brown; legs dark brown with all tarsi yellowish.

Forewing with first recurrent vein interstitial with first transverse cubital. Scattered long white hairs on frons, vertex, posterior genae, sides of thorax and propodeum, legs, venter; long, golden hairs on gastral tergum 5.

Male

Length about 5.5 mm; wing length about 4.0 mm. Relative head measurements: width 7.6; length 8.4;

clypeal length 2.6; lower interocular distance 4.4; upper interocular distance 5.2; interantennal distance 1.3; antennocular distance 0.9; interocellar distance 2.0; ocellocular distance 1.1, ocelloccipital distance 0.4. Anterior margin of clypeus broadly truncate, upper margin of clypeus slightly concave; labial palps as in female; inner hind tibial spur ciliate; horizontal zone of propodeum longer than metanotum; frons above antennae dullish, covered with very close reticulation, punctures not obvious. Colour as in female with fore femora yellowish anteriorly. Forewing as in female. Scattered long white hairs on frons, vertex, clypeus, antennal scapes, mandibles, posterior genae, sides of thorax and propodeum, legs.

Terminalia (Figures 20, 21, 31, 32, 40, 41). The seventh gastral sternum (Figures 31, 32) has long branched hairs on only two lobes.

Etymology

The species is named from the type locality.

Euryglossa (Euhesma) scoparia sp. nov.

Figures 2, 49

Material Examined

Holotype

♀, N Middleback Range, South Australia, 137°09'E 33°03'S, 7–8 October 1973, on *Eremophila scoparia*, C.A. & T.F. Houston (WAM).

Paratypes

Australia: Western Australia: 1 ♀, same data as holotype (WAM); 1 ♀, 4.5 km NNE of Mt Jackson (119°07'E 30°59'S), 5–11 September 1979, T.F. Houston *et al.*, on flowers of *Eremophila* ?*scoparia* (WAM); 1 ♀, 31°18'S 119°44'E, 6 km E of Yellowdine, 10 October 1981, I.D. Naumann and J.C. Cardale on flowers of *Eremophila* (ANIC).

Other Material

Australia: Western Australia: 2 ♀, 18 km WSW Mulline, 29°51'S 120°20'E, 23 September 1982, B. Hanich and T.F. Houston, on flowers of *Eremophila pantonii* (WAM).

Description

Female

Length about 6.0 mm; wing length about 4.5 mm. Relative head measurements: width 7.5; length 9.5; clypeal length 3.0; lower interocular distance 4.2; upper interocular distance 5.0; clypeo-antennal distance 0.8; interantennal distance 1.4; antennocular distance 0.9; interocellar distance 1.9; ocellocular distance 1.4; ocelloccipital distance 0.2. Upper margin of clypeus straight, labial palps



Figures 8–13 *Euryglossa* (*Euhesma*) species. 8, Head of *E. macrayae* ♂; 9, Apex of tibia and base of tarsus of foreleg of *E. pantoni* ♂ (× 260); 10, Hind tibial spurs of *E. nalbarra* ♀ (× 260); 11, Hind tibia of *E. coppinensis* ♂ showing basitibial plate (× 80); 12, Distitarsus and claw of midleg of *E. macrayae* ♀ (× 280); 13, Head of *E. pantoni* ♂.

(Figure 2) longer than maxillary palps, with segments in increasing lengths 2 (very small), 1, 3, 4; malar space distinct; horizontal zone of propodeum longer than metanotum; clypeus with a slight median longitudinal furrow and punctures wide apart. Labial palp segment 1 dark brown, segments 2–4 yellowish; legs dark brown.

Etymology

The specific name refers to the species of *Eremophila* on which the types were taken.

***Euryglossa (Euhesma) sturtiensis* sp. nov.**

Figures 39, 45, 49

Material Examined

Holotype

♀, 30 km along Haasts Bluff Road, Northern Territory, 23°29'17"S 132°07'41"E 11 October 1995, K. Walker, on *Eremophila* (MV).

Paratypes

Australia: Northern Territory: 9 ♀, 4 ♂, same data as holotype (UQIC, ANIC, MV).

Other Material

Australia: Northern Territory: 1 ♀, 11 ♂, 41 km N Hermansberg, 23°49'29"S 132°25'37"E, 9 October 1995, K. Walker on *Eremophila sturtii*; 7 ♀, 3 km N Running Waters, 24°17'10"S 132°54'50"E, 15 October 1995, K. Walker, on *Eremophila*; 1 ♀, 2 ♂, Illamurta Springs, 24°18'S 132°31'E, 10 October 1994, K. Walker, on *Eremophila* (Finke No. 1028); 2 ♀, 1 ♂, same data at 24°18'31"S 132°41'45"E, on 15 October 1995; 5 ♀, Stokes Creek, Watarrka, 24°24'16"S 131°46'19"E, 19 October 1994, K. Walker, on *Eremophila* (Watarrka No.300); 1 ♂, 91 km N Eridunda, 24°28'00"S 133°18'59"E, 7 October 1995, K. Walker, on *Eremophila*; 6 ♀, 5 ♂, 58 km NE Curtin Springs, 25°06'32"S 132°15'18"E, 19 October 1996, K. Walker & K. Sparks, on *Eremophila* (all in MV). **Queensland:** 40 ♀, Dynevor Lakes, 88 km W Eulo 28°05'S 144°12'E, 27 September 1991, G. Daniels, on *Eremophila sturtii*; 1 ♀, Nine Mile Bore, 16 km E. Eulo 28°07'S 145°11'E, same data (all in UQIC).

Description

Female

Length about 5.0 mm; wing length about 4.0 mm. Relative head measurements: width 6.3; length 7.7; clypeal length 2.2; lower interocular distance 3.6; upper interocular distance 4.2; interantennal distance 1.2; antennocular distance 0.8; interocellar distance 1.4; ocellocular distance 1.2; ocellocipital distance 0.3. Labial palps longer than maxillary

palps with segments in increasing lengths in the order 2, 1, 3, 4; malar space distinct, clypeus and supraclypeal area shining, frons above antennae dull, with close reticulation and wide apart punctures.

Labial palp segments 1 and 2 dark brown, 3 and 4 yellowish; legs dark brown with tibiae and tarsi mainly yellowish. Dorsal surface of gaster variable – in most golden with wide transverse bands of dark brown across segments 1–4.

Forewing with first recurrent vein distal to first transverse cubital.

Male

Length about 4.0 mm; wing length about 3.0 mm. Relative head measurements: width 5.5; length 7.0; clypeal length 2.0; lower interocular distance 3.0; upper interocular distance 3.9; interantennal distance 0.9; antennocular distance 0.6; interocellar distance 1.4; ocellocular distance 1.0; ocellocipital distance 0.2. Labial palps as in female. Colour more yellow (light brown) than female on anterior margin of clypeus, labrum, legs and venter; last gastral tergum polished, yellow. Forewing as in female. Terminalia as in Figures 39 and 45. Eighth gastral tergum with distal shaft short and stout with hairs lateral only.

Remarks

The Queensland specimens (only females known) tend to be larger and more variable in colour than those from the Northern Territory. They may represent another species.

Etymology

The specific name refers to the plant from which some of the specimens were collected.

***Euryglossa (Euhesma) symmetra* sp. nov.**

Figures 4, 49

Material Examined

Holotype

♀, 13 miles (20.8 km) E of Meekatharra, Western Australia, 31 August 1971, T.F. Houston, on blue *Eremophila* (WAM).

Paratype

Australia: Western Australia: 1 ♀, same data as holotype (WAM).

Description

Female

Length about 6.8 mm; wing length about 4.0 mm. Relative head measurements: width 7.8;



Figures 14–19 Head and mouth parts of *Euryglossa* (*Euhesma*) species: 14, *E. nalbarra* ♀; 15, *E. pantoni* ♀; 16, *E. macrayae* ♀; 17, *E. sulcata* ♀; 18, *E. macrayae* ♂; 19, *E. coppinensis* ♂;

length 9.2; lower interocular distance 4.7; upper interocular distance 5.5; interantennal distance 1.6; antennocular distance 1.1; interocellar distance 1.9; ocellocular distance 1.6; ocelloccipital distance 0.4. Clypeus extended well below lower ends of eyes; anterior margin of clypeus indented medianly; labial palps (Figure 4) longer than maxillary palps, segments of increasing length in the order 2, 1, 3, 4, segment 3 broadest; malar space distinct; horizontal zone of propodeum about as long as metanotum; clypeus and supraclypeal area highly polished.

Labial palps with segments 1 and 2 dark brown, segments 3 and 4 golden; legs dark brown with tarsi yellow-brown.

Forewing with first recurrent vein slightly distal to first transverse cubital.

Scattered long white hairs on face, scapes, genae posteriorly, vertex, dorsum of thorax, sides of propodeum; longer scattered white hairs on sides of thorax, legs, posterior half of gastral sterna, long brown hairs on last two gastral terga.

Etymology

The specific name meaning 'similar' refers to the similarity of this species with *nalbarra*.

Group 2

Euryglossa (Euhesma) alicia sp. nov.

Figure 50

Material Examined

Holotype

♀, 53 km E by N of Alice Springs, Northern Territory, 23°35'S 134°22'E, 6 October 1978, J.C. Cardale, on *Eremophila* sp. (ANIC).

Description

Female

Length about 7.0 mm; wing length about 5.0 mm. Relative head measurements: width 8.7; length 10.0; lower interocular distance 5.2; upper interocular distance 5.7; interantennal distance 1.9; antennocular distance 1.0; interocellar distance 1.9; ocellocular distance 1.5. Labial palps longer than head, segments in increasing length in the order 1 = 2, 4, 3, with 1 and 2 dark brown, 3 and 4 ribbon-like and yellowish; fronto-clypeal suture not evident; supraclypeal area flat. Legs dark brown.

Etymology

The specific name refers to the area near which the holotype was taken.

Euryglossa (Euhesma) cuneifolia sp. nov.

Figure 50

Material Examined

Holotype

♀, 16 km WSW of Lyons River Homestead, Western Australia, 24°38'S 115°20'E, 30 August – 1 September 1980, C.A. Howard and T.F. Houston, on *Eremophila cuneifolia* [sic.] Kraenzlin (WAM).

Paratype

Australia: Western Australia: 1♀, same data as holotype (WAM).

Other Material

Australia: Western Australia: 1♀, 14 miles (22.4 km) NE of Newman, 28 August 1971, on *Eremophila* (WAM).

Description

Female

Length about 7.0 mm; wing length about 5.0 mm. Relative head measurements: width 8.5; length 10.0; lower interocular distance 5.3; upper interocular distance 6.0; interantennal distance 1.9; antennocular distance 1.1; interocellar distance 2.0; ocellocular distance 1.5. Anterior margin of clypeus slightly indented; fronto-clypeal suture faint; facial foveae wide, shallow; malar space short; frontal line distinct; frons above antennae dull with fine reticulation and sparse punctures; clypeus and supraclypeal area shining; foveae of second tergum of gaster difficult to see, about as wide as long; labial palp segments in increasing lengths 1 = 2, 3, 4, with segments 3 and 4 ribbon-like.

Labial palps with segments 1 and 2 dark brown, segments 3 and 4 yellowish; legs dark brown with tibiae and tarsi golden; dorsal surface of gaster with transparent tergal margins giving almost a banded appearance.

Scattered long white hairs particularly on ventral body surface and legs; dense long golden hairs on gastral tergum 5.

Etymology

The specific name refers to the species of *Eremophila* from which the types were collected.

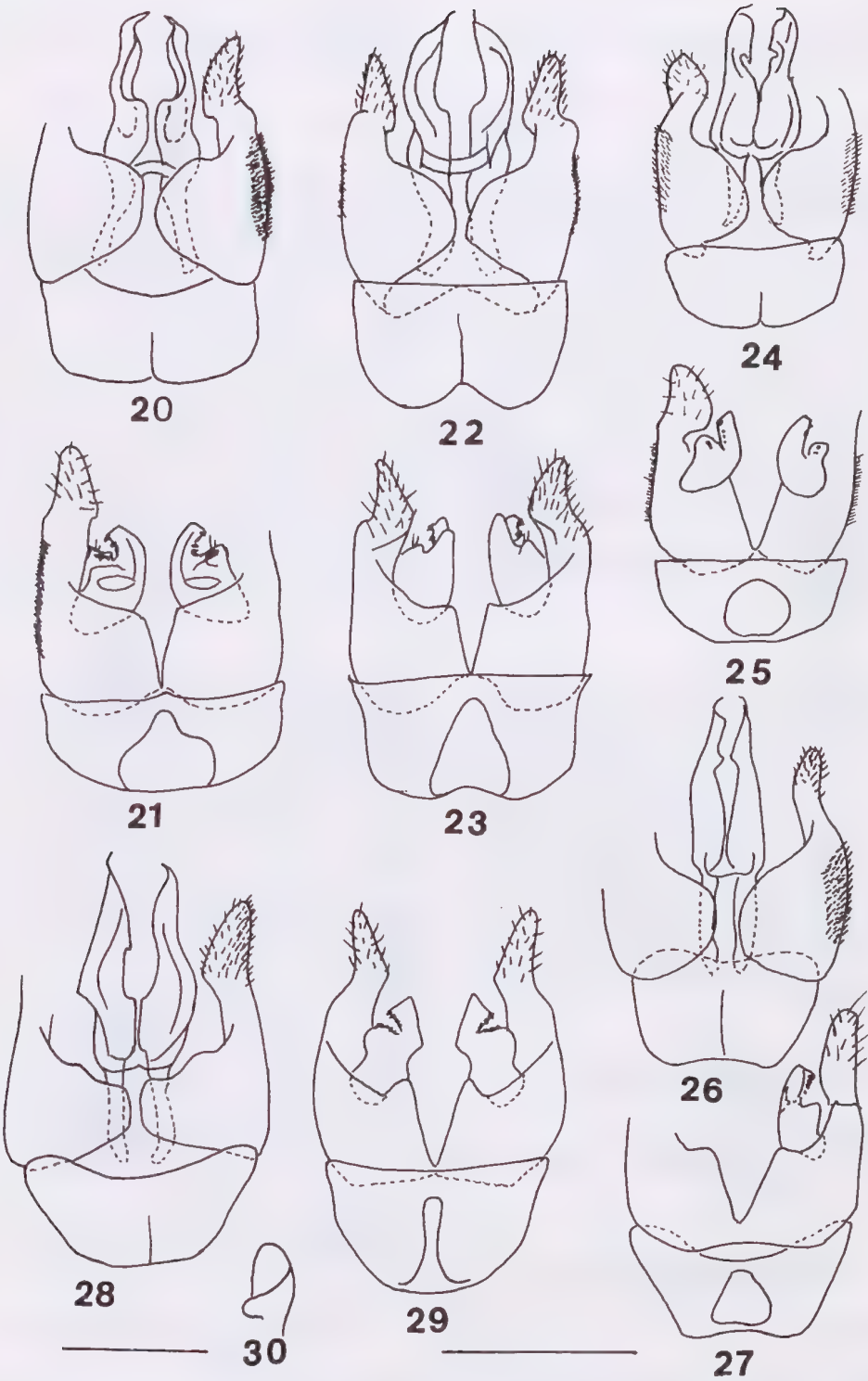
Euryglossa (Euhesma) granitica sp. nov.

Figure 50

Material Examined

Holotype

♀, 22 km S of Mt Magnet, Western Australia, 28°04'S 117°51'E, 6 September 1980, C.A. Howard and T.F. Houston, on flowers of *Eremophila granitica* S. Moore (WAM).



Figures 20–30 Male genitalia of *Euryglossa* (*Euhesma*) species. (20–29 dorsal and ventral views): 20, 21, *E. nalbarra*; 22, 23, *E. leonora*; 24, 25, *E. mieka*; 26, 27, *E. sulcata*; 28, 29, *E. macrayae*; 30, cup-like tip of gonocoxite of *E. coppinensis*. Scale lines = 0.5mm. Line on left refers to Figure 30 only.

Paratypes

Australia: Western Australia: 1 ♀, 2 ♂, same data as holotype (WAM, UQIC).

Description*Female*

Length about 6.0 mm; wing length about 4.0 mm. Relative head measurements: width 7.3; length 9.1; clypeal length 2.7; lower interocular distance 4.7; upper interocular distance 4.8; interantennal distance 1.3; antennocular distance 0.8; interocellar distance 1.5; ocellocular distance 1.3; ocelloccipital distance 0.5. Anterior margin of clypeus truncate, clypeus in side view somewhat convex; frontal line distinct; labial palps as long as head with segments in increasing lengths in the order 2, 1, 3 = 4; basitibial plate with terminal tubercle about 1/3 length of hind tibia; horizontal zone of propodeum longer than metanotum; frons and clypeus shining with punctures quite far apart; almost no sign of fronto-clypeal suture.

Colour dark brown with antennal flagellum anteriorly, labial segments 3 and 4, tibial bases and all tarsi yellowish.

Male

Length about 6.0 mm; wing length about 4.0 mm. Relative head measurements: width 7.7; length 8.7; clypeal length 2.4; lower interocular distance 4.8; upper interocular distance 5.2; clypeo-antennal distance 0.7; interantennal distance 1.2; antennocular distance 1.1; interocellar distance 1.7; ocellocular distance 1.6; ocelloccipital distance 0.6. Anterior margin of clypeus truncate; frontal line distinct; labial palps as in female, basitibial plate surrounded by a carina, about 1/5 length of hind tibia. Dark brown with antennal flagellum anteriorly, labial segments 3 and 4, tibial bases and all tarsi yellowish. Clypeus dorsally with many long white hairs.

Remarks

This species is very similar to *E. meeka*.

Etymology

Its name refers to the species of *Eremophila* from which it was collected.

Euryglossa (Euhesma) meeka sp. nov.

Figures 5, 24, 25, 34, 43, 50

Material Examined*Holotype*

♀, 13 miles (20.8 km) E of Meekatharra, Western Australia, 31 August 1971, T.F. Houston, on blue *Eremophila* (WAM).

Paratypes

Australia: Western Australia: 1 ♀, 8 ♂, same data as holotype (WAM, UQIC).

Description*Female*

Length about 6.0 mm; wing length about 4.0 mm. Relative head measurements: width 7.7; length 9.2; clypeal length 2.7; lower interocular distance 4.8; upper interocular distance 5.2; clypeo-antennal distance 0.7; interantennal distance 1.5; antennocular distance 1.1; interocellar distance 1.8; ocellocular distance 1.5; ocelloccipital distance 0.6. Anterior margin of clypeus broadly truncate, fronto-clypeal suture evident; frontal line distinct; labial palps (Figure 5) as long as head, with segments in increasing lengths in the order 2, 1, 4, 3; horizontal zone of propodeum longer than metanotum; frons above antennae not dull, covered with fine reticulation and sparse punctures; clypeus crumpled looking with indistinct median longitudinal furrow.

Labial palps with segments 1 and 2 dark brown, segments 3 and 4 pale yellow; legs dark brown with fore tibiae anteriorly and all tarsi golden.

Male

Length about 5.5 mm; wing length about 3.8 mm. Relative head measurements: width 7.7; length 8.5; clypeal length 2.4; lower interocular distance 4.5; upper interocular distance 5.0; interantennal distance 1.2; antennocular distance 1.1; interocellar distance 1.7; ocellocular distance 1.3; ocelloccipital distance 0.7. Frontal line distinct; upper margin of clypeus faint, almost straight; labial palps as in female; facial foveae indistinct; basitibial plate margined by incomplete carinae, about 1/4 length of hind tibia; inner hind tibial spur finely pectinate; horizontal zone of propodeum longer than metanotum; frons above antennae dullish, covered with close reticulation and scattered punctures; clypeus with median longitudinal furrow in basal half; foveae of second segment of gaster indistinct. Scattered long white hairs on clypeus, mandibles, scapes, posterior genae, vertex, dorsum of thorax, sides of thorax, legs, posterior margins of gastral sterna 3–5. Terminalia as in Figures 24, 25, 34, 43.

Etymology

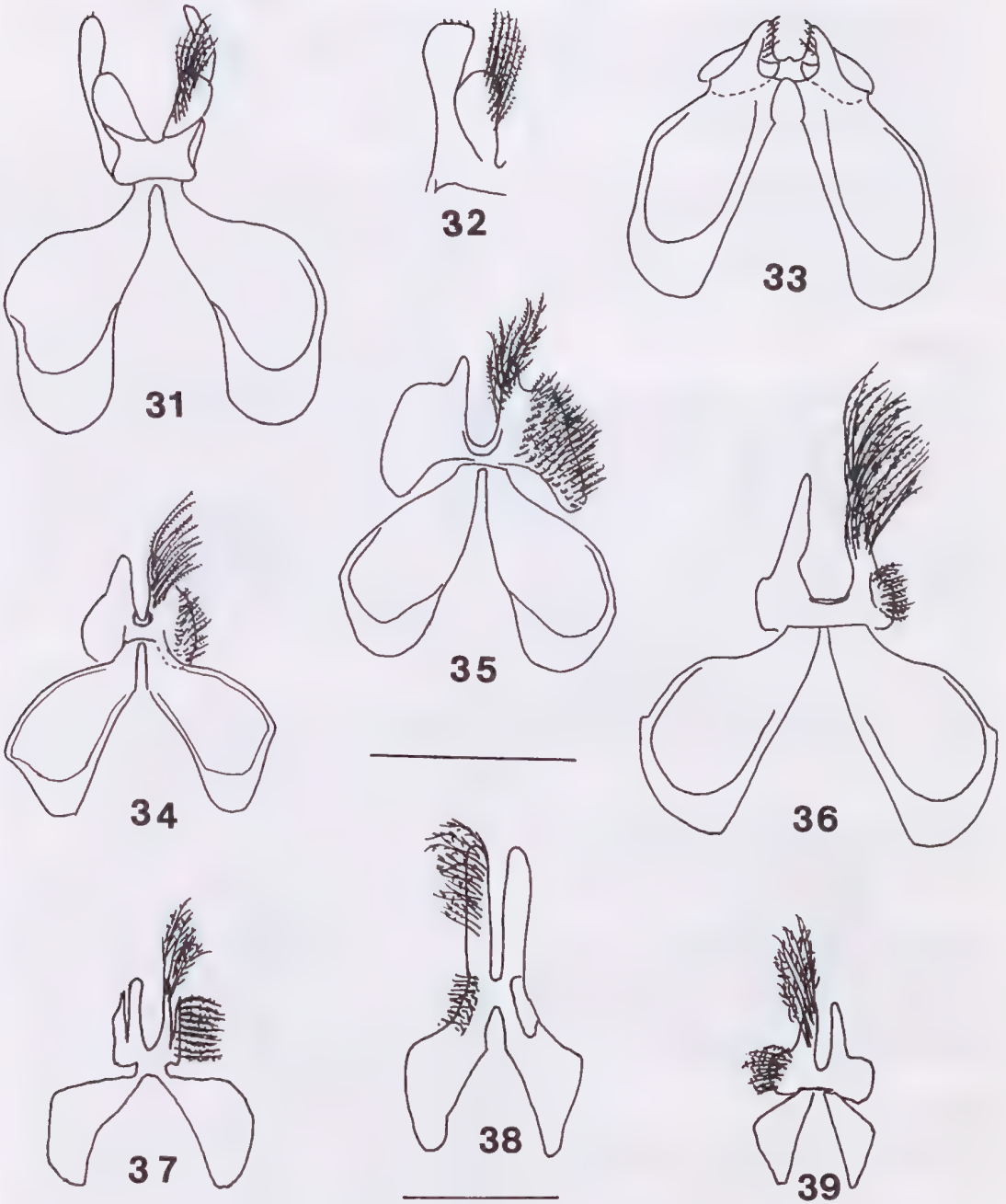
The specific name refers to 'Meekatharra' the type locality.

Euryglossa (Euhesma) pantoni sp. nov.

Figures 9, 13, 15, 50

Material Examined*Holotype*

♀, 18 km WSW Mulline, Western Australia,



Figures 31-39 Seventh gastral sternum of males of *Euryglossa* (*Euhesma*) species (31, 33-39 ventral view with pubescence omitted on one side; 32, lateral view). 31, 32, *E. nalbarra*; 33, *E. leonora*; 34, *E. meeka*; 35, *E. sulcata*; 36, *E. macrayae*; 37, *E. balladonia*; 38, *E. coppinensis*; 39, *E. sturtiensis*. Scale lines = 0.5mm. Upper line refers to Figures 31-36; lower line refers to Figures 37-39.

29°51'S 120°20'E, 23 September 1982, B. Hanich and T.F. Houston, on *Eremophila pantonii* (WAM).

Paratypes

Australia: Western Australia: 6 ♀, 4 ♂, same data as holotype; 2 ♀, 5 ♂, Meleya Well 28°58'S 117°12'E, Thundelarra Station, 28 August – 2 September 1981, T.F. Houston, on *Eremophila pantonii* (WAM, UQIC, ANIC).

Other Material

Australia: Western Australia: 15 ♂, 50 km E of Leonora, 28°51'S 121°50'E, 10 September 1982, B. Hanich and T.F. Houston, on *Eremophila pantonii* (WAM); 1 ♂, Talling Station, September 1976, R.P. McMillan (WAM).

Description

Female

Length about 6.0 mm; wing length about 5.0 mm. Relative head measurements: width 7.2; length 9.0; length labial palp approximately 10.0; lower interocular distance 4.6; upper interocular distance 4.9; interantennal distance 1.4; antennocular distance 1.0; interocellar distance 1.8; ocellocular distance 1.3; ocelloccipital distance 0.7. Fronto-clypeal suture indistinct, labial palp segments of increasing lengths in the order 1, 2, 4, 3, with 1 and 2 dark brown, 3 and 4 ribbon-like, whitish, segment 3 expanded basally (Figure 15), malar space evident; dorsum of head covered with fine reticulation, shining; supraclypeal area and clypeus medianly concave and brilliantly shining. Legs dark brown with distal end of femora, fore tibiae and all tarsi pale yellowish.

Male

Similar to female with more extensive long white hair on body. In specimens from Leonora, the gastral tergum 6 is wholly yellow (partially so in others).

Remarks

My theory that species of *Eremophila* are attended by bee species with mouthparts suitably modified is shaken by this species. It was taken at the same time as the species *E. leonora* which shows no marked lengthening of head or labial palps.

Etymology

The specific name refers to the species of *Eremophila* from which the bees were collected.

Euryglossa (Euhesma) sulcata sp. nov.

Figures 6, 17, 26, 27, 35, 44, 50

Material Examined

Holotype

♀, 85 miles (136 km) NNE of Meekatharra,

Western Australia, 30 August 1971, T.F. Houston, on blue *Eremophila* (WAM).

Paratypes

Australia: Western Australia: 9♀, 2♂, same data as holotype (WAM, UQIC).

Description

Female

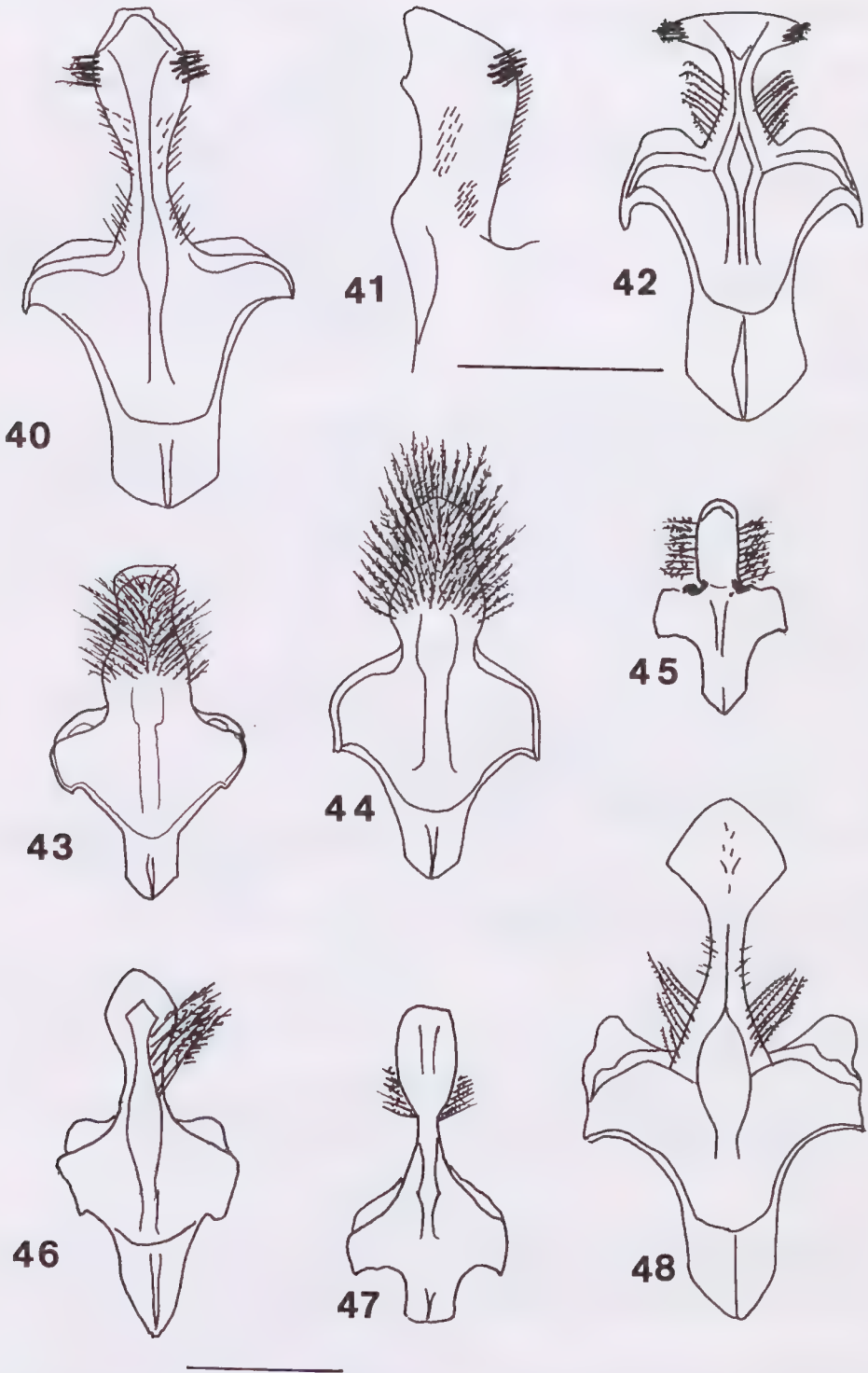
Length about 6.5 mm; wing length about 4.5 mm. Relative head measurements: width 8.0; length 9.5; clypeal length 2.3; lower interocular distance 5.2; upper interocular distance 5.4; clypeo-antennal distance 0.4; interantennal distance 1.9; antennocular distance 1.0; interocellar distance 1.8; ocellocular distance 1.5; ocelloccipital distance 1.0. Anterior margin of clypeus indented medianly, upper margin of clypeus indistinct, almost straight; clypeus with median longitudinal furrow; labial palps (Figures 6, 17) as long as head, segments of increasing length in the order 1 = 2, 3, 4, segments 1 and 2 dark brown, segments 3 and 4 expanded, ribbon-like, golden; horizontal zone of propodeum longer than metanotum; frons above antennae covered with close reticulation and sparse punctures, interspaces shining; clypeus and supraclypeal area shining. Legs dark brown with tarsi golden.

Male

Length about 5.5 mm; wing length about 4.2 mm. Relative head measurements: width 8.9; length 9.0; clypeal length 2.4; lower interocular distance 5.7; upper interocular distance 6.0; clypeo-antennal distance 0.4; interantennal distance 1.7; antennocular distance 1.4; interocellar distance 2.0; ocellocular distance 1.6; ocelloccipital distance 1.1. Anterior margin of clypeus slightly indented medianly, upper margin of clypeus indistinct, slightly concave; clypeus with median longitudinal furrow; labial palps as in female; facial foveae broad, shallow depressions, indistinct; basitibial plate margined by incomplete carinae and tubercles, about 1/3 length of hind tibia; inner hind tibial spur finely pectinate; horizontal zone of propodeum longer than metanotum; frons above antennae covered with close reticulation, punctures more numerous and closer together than in female; foveae of second tergum of gaster indistinct. Colour as in female with fore tibiae golden. Terminalia as in Figures 26, 27, 35, 44.

Etymology

The specific name is from Latin and refers to the furrow medianly on the clypeus.



Figures 40–48 Eighth gastral sternum of males of *Euryglossa* (*Euhesma*) species (40, 42–48, ventral view; 41, lateral view). 40, 41, *E. nalbarra*; 42, *E. leonora*; 43, *E. meeka*; 44, *E. sulcata*; 45, *E. sturtiensis*; 46, *E. balladonia*; 47, *E. coppinensis*; 48, *E. macrayae*. Scale lines = 0.5mm. Lower line refers to Figures 45–47 only.

Euryglossa (Euhesma) wiluna sp. nov.

Figure 50

Material Examined*Holotype*

♀, 26 miles (41.6 km) SSE of Wiluna, Western Australia, 1 September 1971, T.F. Houston, on blue *Eremophila* (WAM).

Paratypes

Australia: Western Australia: 3♀, same data as holotype (WAM, UQIC).

Description*Female*

Length about 6.0 mm; wing length about 4.0 mm. Relative head measurements: width 7.5; length 9.5; clypeal length 2.4; lower interocular distance 4.5; upper interocular distance 5.2; clypeo-antennal distance 0.4; interantennal distance 1.5; antennocular distance 1.1; interocellar distance 1.9; ocellocular distance 1.4. Anterior margin of clypeus slightly indented, upper margin of clypeus concave; malar space very short; frons above antennae with close reticulation and sparse punctures; foveae of second tergum of gaster about 3/5 as wide as long; labial palp segments in increasing lengths 1 = 2, 3, 4 with segments 1 and 2 dark brown, segment 3 and basal 2/3 of 4 ribbon-like and yellowish; clypeus shining; supraclypeal area shining, concave. Legs mostly dark brown with tarsi golden.

Remarks

This species is very similar to *E. yellowdinensis* except in size. Until males are discovered, their relationship remains uncertain.

Etymology

The specific name refers to the type locality.

Euryglossa (Euhesma) yellowdinensis sp. nov.

Figure 50

Material Examined*Holotype*

♀, 31°18'S 119°44'E, 6 km E of Yellowdine, Western Australia, 10 October 1981, I.D. Naumann, J.C. Cardale, on flowers of *Eremophila* (ANIC).

Paratypes

Australia: Western Australia: 6♀, 17♂, same data as holotype (ANIC, WAM, UQIC); 1 ♀, same data as holotype on *Melaleuca* (ANIC).

Description*Female*

Length about 5.0 mm; wing length about 4.00 mm. Relative head measurements: width 6.9; length 7.5; clypeal length 2.3; lower interocular distance 3.8; upper interocular distance 4.7; clypeo-antennal distance 0.3; interantennal distance 1.3; antennocular distance 0.9; interocellar distance 1.6; ocellocular distance 1.2; ocelloccipital distance 0.4. Labial palps as long as head with segments of increasing lengths in the order 1, 2, 3, 4 with 1 and 2 dark brown and 3 and 4 ribbon-like, yellowish. Legs dark brown with fore tibiae anteriorly and all tarsi golden.

Male

Length about 4.0 mm; wing length about 3.0 mm. Relative head measurements: width 6.3; length 6.7; clypeal length 1.5; lower interocular distance 3.4; upper interocular distance 4.2; clypeo-antennal distance 0.6; interantennal distance 1.2; antennocular distance 0.7; interocellar distance 1.6; ocellocular distance 0.7. Colour as in female with more yellow on legs (mid tibiae anteriorly and bases of all tibiae).

Etymology

The specific name refers to the only locality known for this species.

Group 3*Euryglossa (Euhesma) coppinensis* sp. nov.

Figures 19, 30, 38, 47, 51

Material Examined*Holotype*

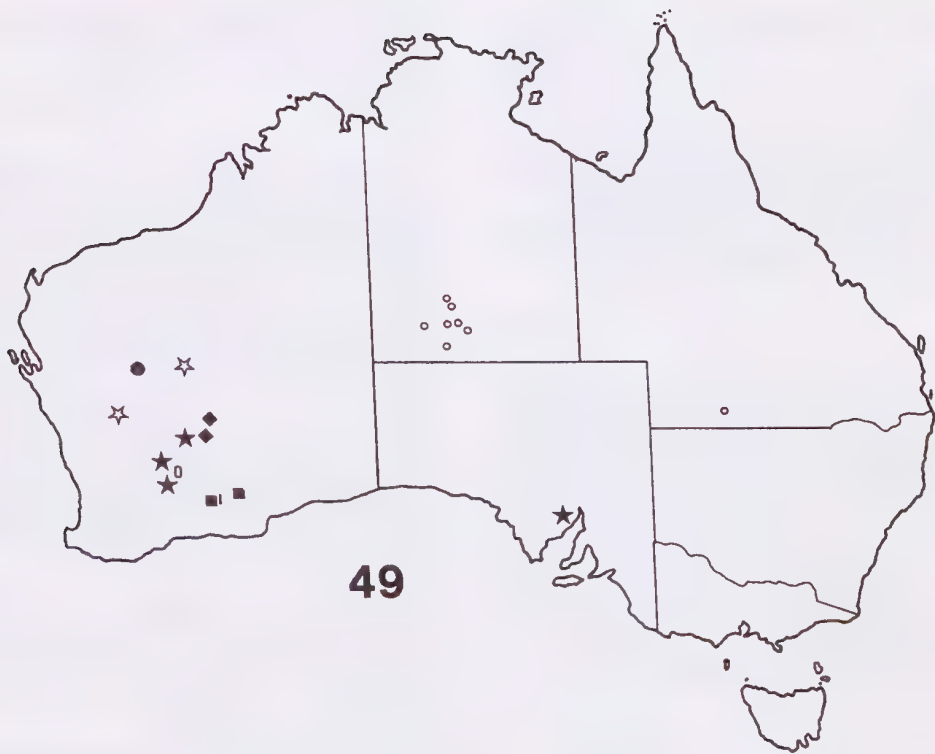
♀, Coppin Pool area, 30 km S of Mt Bruce, NW Div., Western Australia, 10–13 May 1980, T.F. Houston *et al.*, on flowers of *Eremophila* (WAM).

Paratypes

Australia: Western Australia: 9 ♂, same data as holotype (WAM, UQIC).

Description*Female*

Length about 6.0 mm; wing length about 4.5 mm. Relative head measurements: width 9.0; length 9.0; clypeal length 2.8; lower interocular distance 5.6; upper interocular distance 5.9; clypeo-antennal distance 0.4; interantennal distance 2.0; antennocular distance 1.2; interocellar distance 1.8; ocellocular distance 1.6. Anterior margin of clypeus broadly truncate; upper margin of clypeus faint, slightly concave; labial palps exceedingly elongate,



49



50



51

Figures 49–51 49 Known distribution of *Euryglossa* (*Euhesma*.) species. Group 1. ○ *E. atra*; | *E. aurata*; ■ *E. balladonia*; ◆ *E. leonora*; ☆ *E. nalbarra*; ★ *E. scoparia*; ○ *E. sturtiensis*; ● *E. symmetra*. 50 Known distribution of *Euryglossa* (*Euhesma*) species. Group 2. ★ *E. alicia*; ■ *E. cuneifolia*; ○ *E. granitica*; ○ *E. meeka*; ● *E. pantoni*; ▼ *E. sulcata*; ▽ *E. wiluna*; ▴ *E. yellowdinensis*. 51 Known distribution of *Euryglossa* (*Euhesma*) species. Group 3. ○ *E. coppinensis*; ■ *E. macrayae*; ★ *E. newmanensis*; ● *E. walkeri*.

longer than head, segments in increasing length in the order 1, 4, 3, 2 with 2, 3 and 4 flattened, ribbon-like and apparently channelled medianly; horizontal zone of propodeum longer than metanotum.

Labial palps with segment 1 dark brown, segments 2, 3, 4 yellowish with 2 infused with brown. Legs dark brown with tarsi yellowish.

Long white hairs on clypeus, frons, posterior genae, mesoscutum, scutellum, metanotum, sides of propodeum, sides of thorax, legs, venter.

Male

Length about 6.0 mm; wing length about 4.5 mm. Relative head measurements (Figure 19): width 9.0; length 8.0; clypeal length 2.0; lower interocular distance 6.0; upper interocular distance 6.0; clypeo-antennal distance 0.2; interantennal distance 2.0; antennocular distance 1.4; interocellar distance 1.9; ocellocular distance 1.5. Anterior margin of clypeus gently convex; upper margin of clypeus not clear; facial foveae not evident; labial palps as in female; horizontal zone of propodeum longer than metanotum. Colour as in female, with labial palps with segment 1 dark brown, segment 2 brown, segments 3 and 4 yellowish. Terminalia as in Figures 30, 38 and 47.

Remarks

This is the only species in which the head of the female is not longer than wide. The head of the male is wider than long. The cup-like tip of the gonostylus of the genitalia (Figure 30) has not been seen elsewhere.

Etymology

The specific name refers to the type locality.

Euryglossa (Euhesma) macrayae sp. nov.

Figures 7, 8, 12, 16, 18, 28, 29, 36, 48, 51

Material Examined

Holotype

♀, 85 miles (136 km) NNE of Meekatharra, Western Australia, 30 July 1971, T.F. Houston, on blue *Eremophila* (WAM).

Paratypes

Australia: Western Australia: 10 ♀, 5 ♂, same data as holotype (WAM, UQIC, ANIC).

Other Material

Western Australia: 7♀, 8 km S of Lyons River Homestead, 24°38'S 115°20'E, 30 August 1980, on *Eremophila platycalyx* var. *lancifolia* (WAM 341-1); 2♀, same data, 16 km WSW of Lyons River Homestead, 30 August – 1 September 1980, on

Eremophila cuneifolia Kraenzlin (WAM 344-11); 1♀, same data on pink *Eremophila* (WAM 344-13).

Description

Female

Length about 7.0 mm; wing length about 5.0 mm. Relative head measurements: width 9.5; length 10.4, clypeal length 3.3; lower interocular distance 6.0; upper interocular distance 6.6; interantennal distance 2.2; antennocular distance 1.5; interocellar distance 2.0; ocellocular distance 1.9; ocelloccipital distance 0.8. Anterior margin of clypeus indented medianly, upper margin of clypeus slightly concave; labial palps (Figures 7, 16) exceedingly elongate, longer than head, segment 1 shortest, segments 2, 3, 4 about equal; facial foveae broad shallow depressions nearly 1/2 length of eyes; malar space short; horizontal zone of propodeum about as long as metanotum; clypeus shining; foveae of second segment of gaster about 1 1/2 times as long as wide.

Labial palps with segment 1 dark brown, segment 2 with basal half dark brown, distal half golden brown, segments 3 and 4 with basal half whitish, distal half golden brown; legs with coxae and trochanters black, all femora dark brown, tibiae and tarsi yellowish-brown.

Scattered long yellowish hairs on frons above antennae, vertex, clypeus, clypeal margin; shorter white hairs on dorsum of thorax, sides of propodeum; longer scattered white hairs on posterior genae, sides of thorax, legs, gastral sterna; long yellowish hairs on gastral terga 5 and 6.

Male

Length about 6.0 mm; wing length about 4.8 mm. Relative head measurements: width 7.3; length 7.3; clypeal length 2.1; lower interocular distance 4.6; upper interocular distance 5.1; clypeo-antennal distance 0.6; interantennal distance 1.4; antennocular distance 1.2; interocellar distance 1.4; ocellocular distance 1.4; ocelloccipital distance 0.9. Anterior margin of clypeus indented medianly, upper margin of clypeus slightly concave; labial palps (Figure 18) as in female; facial foveae broad, shallow, indistinct; malar space short; inner hind tibial spur finely pectinate; horizontal zone of propodeum about as long as metanotum; foveae of second segment of gaster about 3 times as long as wide. Colour as in female except legs orange with coxae black. Scattered long white hairs on frons, clypeus, mandibles, vertex, posterior genae, dorsum of thorax; longer scattered white hairs on sides of thorax, legs, venter. Terminalia as in Figures 28, 29, 36, 48.

Remarks

Although the specimens from Lyons River

area were taken from different species of *Eremophila*, I cannot separate them. None is as robust as the specimens from Meekatharra and when males are known a different species may be indicated.

Etymology

This species is named for my niece Elizabeth McCray whose typing skills greatly helped preparation of this manuscript.

Euryglossa (*Euhesma*) *newmanensis* sp. nov.

Figure 51

Material Examined

Holotype

♀, 14 miles (22.4 km) NE of Newman, Western Australia, 28 August 1971, T.F. Houston, on *Eremophila* (WAM).

Paratype

Australia: Western Australia: ♀, same data as holotype (WAM).

Description

Female

Length about 7.0 mm; wing length about 5.0 mm. Relative head measurements: width 8.9; length 10.1; clypeal length 2.9; lower interocular distance 5.9; upper interocular distance 6.1; interantennal distance 2.0; antennocular distance 1.2; interocellar distance 2.0; ocellocular distance 1.6. Labial palps as long as head with segment 1 shortest, segments 2, 3, 4 about equal in length.

Etymology

The specific name refers to the type locality.

Euryglossa (*Euhesma*) *walkeri* sp. nov.

Figure 51

Material Examined

Holotype

♀, 40 km N of Norseman, Western Australia, 31°52'S 121°47'E, 20 November 1989, K.L. Walker, on *Eremophila* (MV).

Paratypes

Australia: Western Australia: 2♀, same data as holotype, 5♀, 35 km E of Norseman, 32°12'S 122°04'E, 30 October 1989, K.L. Walker, on *Eremophila*; 1♀, 31 km S Norseman, 32°27'S

121°47'E, 31 October 1989, K.L. Walker, on *Eremophila* (MV, UQIC).

Other Material

Western Australia: 1♀, 31°07'S 121°24'E, 29 km SE by E of Coolgardie, 11 October 1981, (ANIC); 2♀, So[uthern] Cross, 19 November 1979, on *Eucalyptus* (RMBM); 1♀, 70–75 km ENE of Norseman, 10–16 November 1978, on flowers of *Eremophila scoparia* (WAM).

Description

Female

Length about 4.5 mm; wing length about 3.0 mm. Relative head measurements: width 6.3; length 7.0; clypeal length 1.8; lower interocular distance 3.4; upper interocular distance 4.1; interantennal distance 1.4; antennocular distance 0.5; interocellar distance 1.4; ocellocular distance 1.1. Upper margin of clypeus straight; labial palps longer than head, segments in increasing length in the order 1, 4, 3, 2 with 1 and 2 cylindrical and widest. Frons above antennae with obvious evenly-spaced punctures and very distinct frontal line; supraclypeal area and clypeus shining, concave, with fewer punctures.

Labial palps with segments 1 and 2 dark brown, 3 and 4 yellowish. Legs dark brown with tibiae and tarsi golden.

Long white hairs plentiful on ventral body surface and legs.

Etymology

The specific name honours Dr Ken Walker, the collector of this species with whom I've spent many hours collecting and discussing bees.

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Guide to Authors

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Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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The International System of units should be used.

Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

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